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THE UNIVERSITY OF ALBERTA

THE INFLUENCE OF MICROCLIMATE AND GRAZING ON THE GROWTH OF *LATHYRUS OCHROLEUCUS* (HOOK.) IN CENTRAL ALBERTA.

BY

JOHN D. BECKINGHAM

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

DEPARTMENT OF GEOGRAPHY

EDMONTON, ALBERTA

FALL, 1990

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ISBN 0-315-65060-5

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DEGREE: MASTER OF SCIENCE

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SUBMITTED BY: JOHN D. BECKINGHAM

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF SCIENCE.

G.P. Kershaw

G. P. KERSHAW

G. H. HENRY

R. J. HUDSON

DATE: Oct. 2, 1990

Abstract

This study focuses on the autecology of *Lathyrus ochroleucus* Hook. an important forage species for wapiti, deer, and cattle. It is preferentially selected and utilized much in excess of its availability relative to other forbs.

L. ochroleucus is found in forested areas that are considered marginally-arable. These areas are important habitat for ungulates and their use for cattle and game ranching is increasing. With increased resource development such as agricultural expansion, oil exploration, and forestry and mining activities it becomes more important to properly manage this limited rangeland resource. A better understanding of the autecology of *L. ochroleucus* will assist in formulating management strategies to maximize its utilization while at the same time maintaining its production.

The growth of 325 plants (ramets) was monitored throughout the 1989 growing season in three plots located within the Cooking Lake Moraine at the Ministik Wildlife Research Station (35 km ESE of Edmonton, Alberta). Temperature and soil moisture data were collected and analyzed in an effort to determine their influence on *L. ochroleucus* growth. At each of the three plots, approximately 2/3 of the plants were clipped to 25 cm in an effort to simulate grazing. The affect of grazing on the growth and production of *L. ochroleucus* was evaluated.

Plant height was not a dominant factor influencing the growth of *L. ochroleucus* except early in the growing season (6 May to 18 May).

The mesoclimatic influences of the regional weather patterns were approximately 21 times stronger in their influence on *L. ochroleucus* growth than the microclimatic differences among sample sites. This suggests that official meteorological records which reflect mesoscale climate may be usefully applied in the evaluation of *L. ochroleucus* growth.

The temperature regime during the study significantly affected the growth of *L. ochroleucus*. Growth rate of *L. ochroleucus* had a Q_{10} of

2.56 which indicates that its growth rate is a chemically controlled process. Soil moisture content did not become limiting.

The simulated grazing (clipping) of *L. ochroleucus* plants reduced net production in the aspen-dominated forest because it reduced the number of plants growing. Clipping reduced net production even though the growth rate of the plants that grew increased. *L. ochroleucus* appears to be susceptible to grazing pressures and if utilized early in the growing season its production may be inhibited. Management strategies must therefore incorporate the amount and timing of use of this important forage species, in productivity and ungulate carrying capacity considerations.

ACKNOWLEDGMENTS

This thesis would not have been completed if not for the support and assistance of many people. It is impossible to mention everyone. First I express thanks to my supervisor Peter Kershaw for all his encouragement, assistance and support. He managed to always come through in the nick of time. I would also like to thank other members of my advisory committee, Greg Henry and Bob Hudson for their review of the manuscript and constructive criticism.

As with most masters students, three times more field data was collected than needed. This was made possible through the enormous and much appreciated effort of Shellie Alexander, Kevin Skaret, and brother Jim. Their valiant efforts in navigating quads, speed walking, and battling hornets are commended.

Thanks to my family and friends. Thanks mom, your the **best**! Jim & Sue thanks for the rescue. Dad and Kathy you added inspiration. I would like to thank Iris for her moral support, encouragement, and understandings. She probably feels like she went through the masters program. I would like to thank Lee Weissling for proofreading the manuscript and for his support and friendship.

I would like to acknowledge the financial assistance from the Boreal Institute for Northern Studies. Thanks David Halliwell for freely giving time for discussions.

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1.0 Introduction

This study focuses on the autecology of *Lathyrus ochroleucus* Hook. an important forage species for wapiti, deer, and cattle. It is preferentially selected (Blood, 1966; Weatherill and Keith, 1969; Kufeld, 1973; Hunt, 1979; Watson et al., 1980; Smoliak et al, 1988; Adams et al, 1986) and utilized much in excess of its availability relative to other forbs (Weatherill and Keith, 1969).

L. ochroleucus is found in forested areas that are considered marginally-arable. These areas are important habitat for ungulates and their use for cattle and game ranching is increasing (Ad hoc Committee, 1976). With greater resource development such as agricultural expansion, oil exploration, and forestry and mining activities it is increasingly important to properly manage this limited rangeland resource. A better understanding of the autecology of *L. ochroleucus* will assist in formulating management strategies to maximize its utilization while at the same time maintaining its production.

Proper management requires detailed knowledge of the ecosystem, including the plant species important in herbivore diets. A knowledge of the interaction between an individual plant species and the environment to which it is adapted is an essential prerequisite to the proper management of our rangeland resources (Tueller, 1977; Sosebee, 1977). Tueller (1977) stated that many years ago it was recognized that the welfare of the individual plant is the foundation of the range. However, little quantitative information is available about the effects of environmental factors, including grazing, on the growth and development of the important rangeland species, *L. ochroleucus*.

L. ochroleucus is a climbing, nitrogen-fixing, herbaceous perennial legume of open woods and northern meadows in Boreal white and black spruce forests to lodgepole pine-douglas fir forests, and Aspen Parkland (Moss, 1983). Although *L. ochroleucus* occupies a wide range of habitats, it achieves its greatest abundance in aspen and balsam poplar dominated forests (Moss, 1955). This study was conducted in the Aspen

Parkland of central Alberta, Canada, at Ministik Wildlife Research Station (MWRS).

L. ochroleucus has been described as a decreaser species, sensitive to continued overuse on rangelands (Weatherill and Keith, 1969; Watson et al, 1980; Adams et al, 1986; Smoliak et al, 1988). It may be a preferred forage species due to its high palatability and nutrient content (Adams et al, 1986). Weatherill and Keith (1969) found that *L. ochroleucus* per cent frequency increased under light cattle grazing intensity and decreased under heavy cattle grazing in the aspen parkland. Nietfeld (1983) found *L. ochroleucus* composed approximately 12% of the total bites taken by wapiti in the poplar forest at MWRS. In two studies *L. ochroleucus* has been found to make up a significant portion of the rumen contents of wapiti, composing over 50% of the rumen contents (Blood 1966) and 4.2% of the summer rumen contents (Hunt 1979).

L. ochroleucus was therefore selected for detailed autecological investigation for five reasons:

(1) It is a preferred forage by native ungulates and cattle;

(2) It is a nutritious forage for native ungulates and cattle;

(3) It has a wide distribution (throughout the Boreal, Mixedwood and Parkland ecoregions);

(4) It was virtually unstudied;

(5) It was available for manipulative experimentation at MWRS.

This thesis is presented as five separate but interrelated papers. The chapter following this introduction deals with the physical characteristics of the study area. Chapter three identifies the plant community types found in the study area with the aim of defining the floristic composition of the communities within which *L. ochroleucus* was studied. Chapter four introduces the phenophases of *L. ochroleucus* with the use of a growth curve model. In addition this chapter investigates the relationship between plant height and growth rate. Chapter five evaluates the influence of environmental factors on the growth and production of *L. ochroleucus*. The influence of temperature as an environmental factor is emphasized. In chapter six the effects of a clipping treatment on the growth of *L. ochroleucus* is evaluated. Chapter seven provides a brief overview of the entire research.

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2.0 Study Area

2.1 Introduction

This research was conducted at the Ministik Wildlife Research Station (MWRS) located 35 km ESE of the city of Edmonton, Alberta (SEC 26 TP 50 R21) (Figure 2.1). MWRS was established as a research facility in 1977 by the Department of Animal Science of the University of Alberta in cooperation with Alberta Fish and Wildlife. The station is situated on the Cooking Lake moraine within the Aspen Parkland-Boreal forest transition zone (Zoltai, 1975). MWRS is surrounded by the Ministik Migratory Bird Sanctuary (7,200 ha) which is managed by Ducks Unlimited Canada.

The 250 ha field station is enclosed by a 2.2 m high game fence. The northwest quarter contains corrals, paddocks and facilities used for the intensive management of a research herd of wapiti. In the summer of 1989 the northwest quarter contained 61 wapiti. An additional 16 wapiti along with 23 bison were in the 3/4 section of the game ranch where human contact was minimal. This study was conducted in a portion of the 3/4 section (Figure 2.2).

2.2 Geology and Topography

The Cooking Lake moraine is at an elevation ranging from 710 to 760 m asl, rising 30 to 60 m above the surrounding plain (Bishoff, 1981). A preglacial bedrock high of the underlying Edmonton formation accounts, inpart, for the elevation (Carlson, 1967). The Edmonton formation consists of non-marine shales and sandstones, interbedded with clay ironstone concretionary layers and coal seams (Lang, 1974). During the late Wisconsin period, with the wasting of the stagnating Laurentide ice sheet, thick glacial tills were deposited in the form of ridged and hummocky moraine. Glaciolacustrine sediments from supraglacial lakes are common at any topographic location within the undulating complex of hills and depressions (Crown, 1977). The topography of the study area is illustrated through the use of a Digital Elevation Model (Figure 2.3).

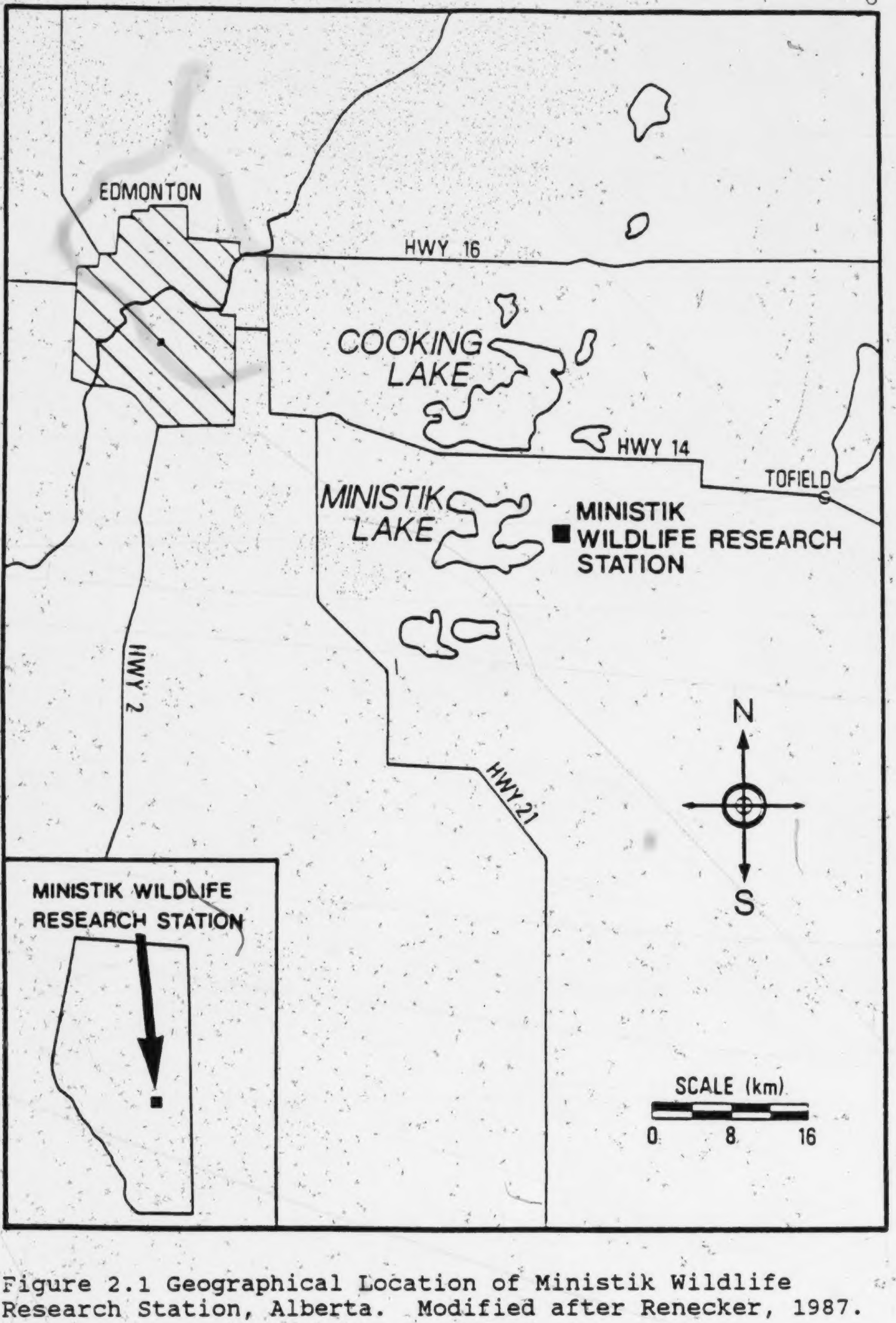

EDMONTON
HWY 16
COOKING LAKE
HWY 14
TOFIELD
MINISTIK LAKE
MINISTIK WILDLIFE RESEARCH STATION
HWY 2
HWY 21
N
S
MINISTIK WILDLIFE RESEARCH STATION
SCALE (km)
0
8
16

Figure 2.1 Geographical Location of Ministik Wildlife Research Station, Alberta. Modified after Renecker, 1987.

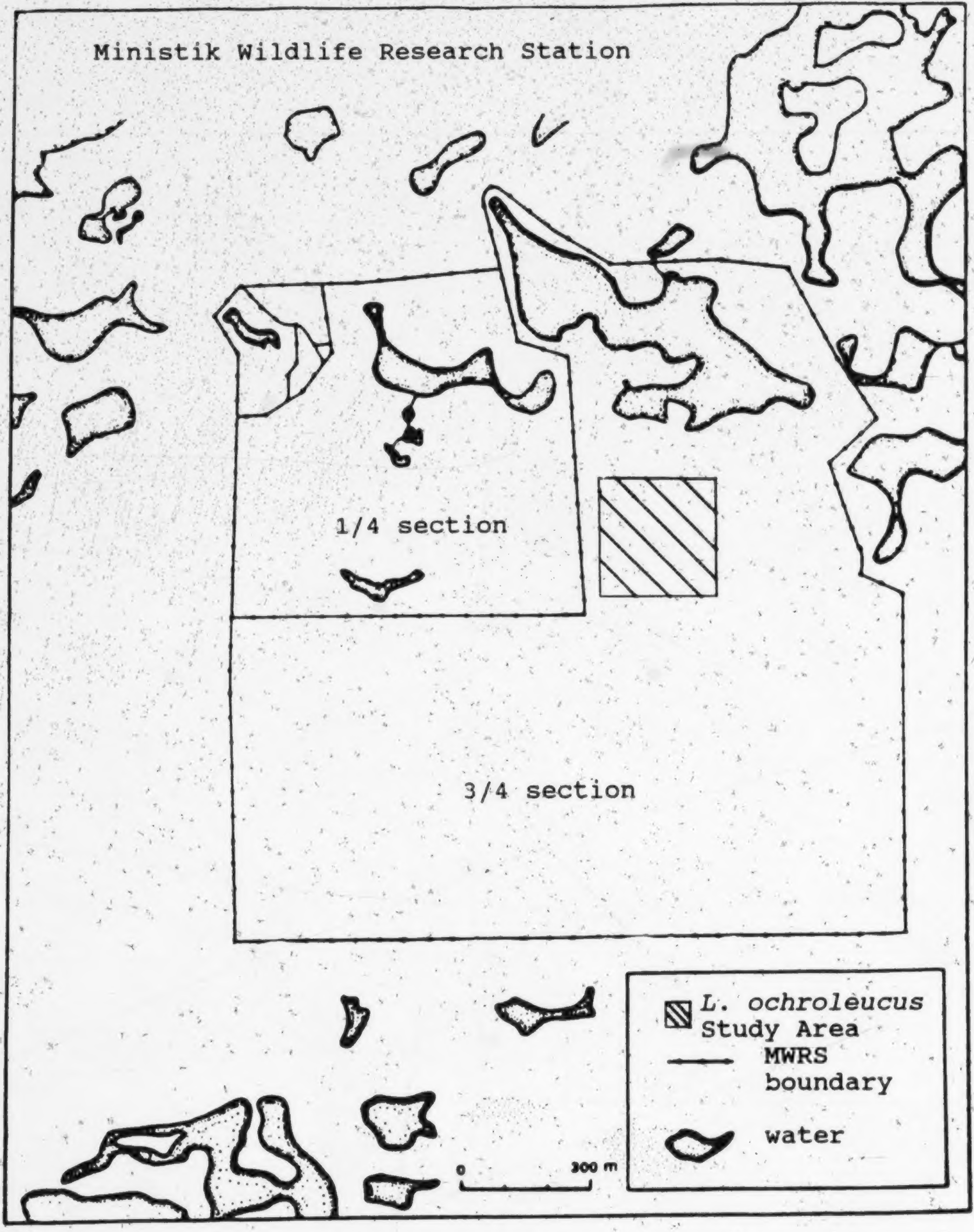
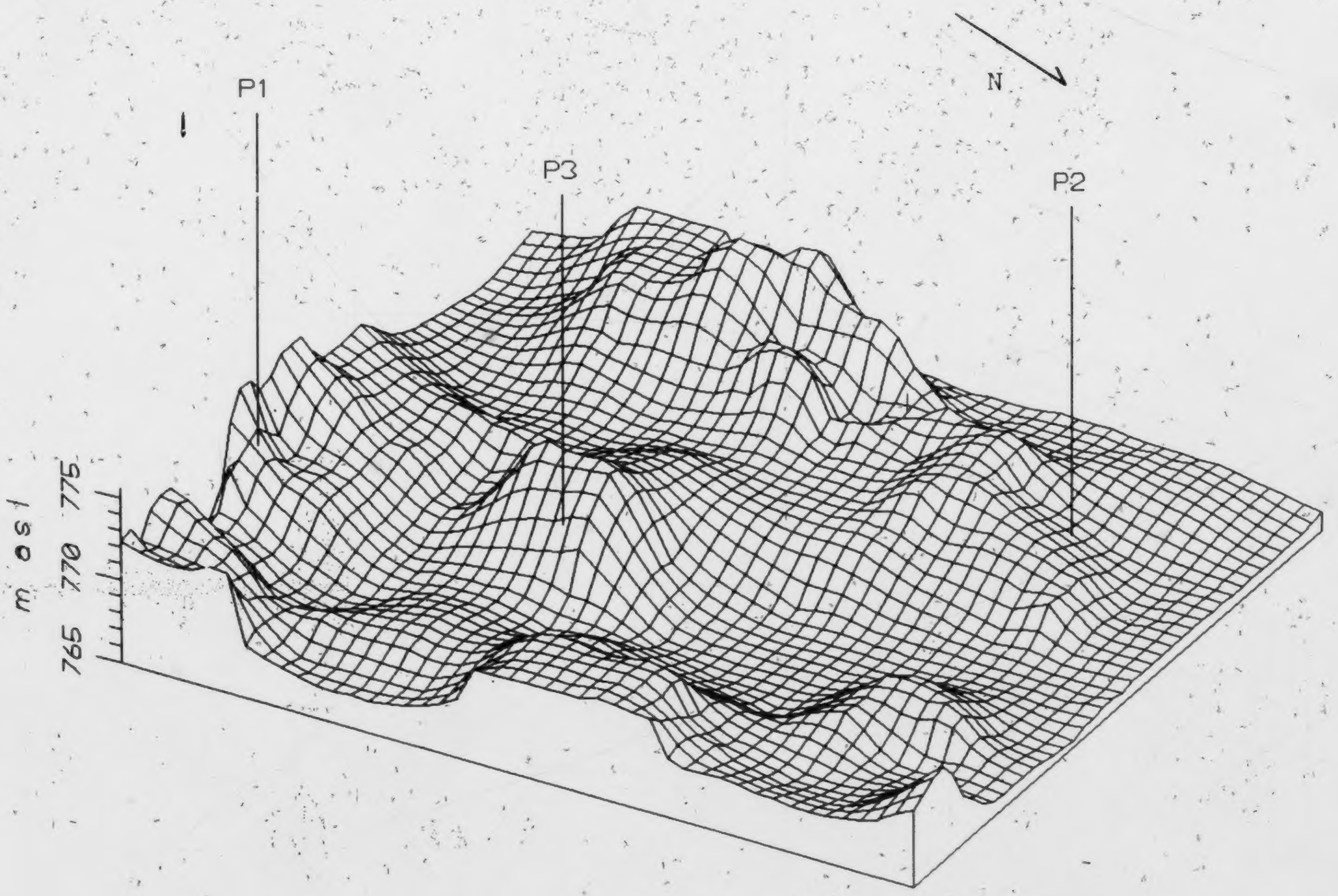

Ministik Wildlife Research Station
1/4 section
3/4 section
L. ochroleucus Study Area
MWRS boundary
water
0
300 m

Figure 2.2 Ministik Wildlife Research Station showing the location of the study area.

Figure 2.3 Digital elevation model of *L. ochroleucus* study sites at MWRS. The three sites where *L. ochroleucus* was studied are labelled P1, P2, and P3. Vertical exaggeration is ten times. The spacing of horizontal lines is ten metres.


N
P1
P3
P2
m asl
765
770
775

2.3 Climate

The climate of the Cooking Lake Moraine area is described as cool continental, sub-arid to sub-humid, with long cold winters and warm summers (Wonders, 1969). Temperatures range from about -40° C to 32° C (Figure 2.4). There are approximately 900 growing-degree-days (>5° C) annually, (Strong and Leggatt, 1981) and an average frost-free period of 100 days (Bishoff, 1981). Normal annual precipitation ranges from 423 mm (Fort Saskatchewan) to 529 mm (Edmonton Stony Plain) within the same micro-climatic zone as the Cooking Lake Moraine (Blyth and Hudson, 1987), with 70% falling as rain during May, June, and July (Bishoff, 1981) (Figure 2.4).

2.4 Soils and Hydrology

Soils of the Ministik area are dominantly Luvisols, which form an island of the Grey Luvisol soil zone within the zone of black soils (Odynsky, 1962). Mineral soils have developed from glacial till and have properties that fall within the limits of the Cooking Lake and Uncas soil series (Crown, 1977). Although the soils have developed on similar parent material under similar climatic conditions, their characteristics differ due to variations in relief, drainage and vegetation.

The soils of Ministik Wildlife Research Station can be arranged in a catenary sequence (Figure 2.5). Well to moderately-drained Orthic Grey Luvisols are the dominant soils of the area (Crown, 1977). These Orthic Grey Luvisols have developed under forest vegetation and occupy the upper and middle slope positions. They have relatively strongly developed Bt horizons overlain by leached, acidic, Ae horizons (Canadian Soil Survey Committee, 1978). These soils, however, are replaced by Dark Grey Luvisols when soil development is strongly influenced by grassland vegetation. Grass vegetation results in the development of dark-coloured Ah horizons, largely caused by additions of organic matter from *in situ* graminoid root decomposition (Pettapeice, 1969). Since the dominant soil forming process in this region is the downward leaching of organic and inorganic soil compounds, the Dark Grey Luvisol has Ah horizons underlain by

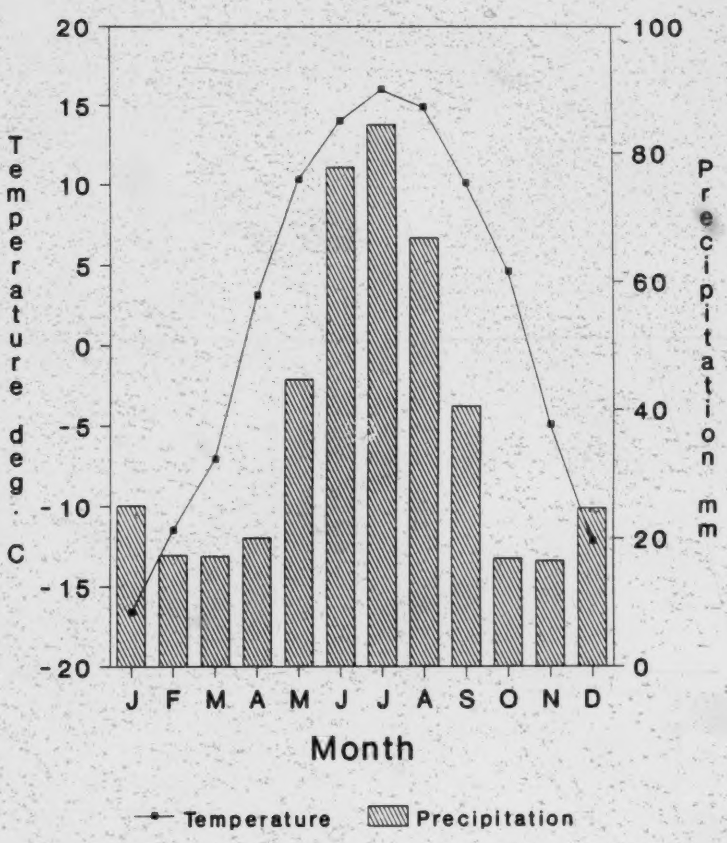


Figure 2.4. Temperature and precipitation normals (1951 to 1980) for Ellerslie climate station located approximately 35 km east of MWRS.

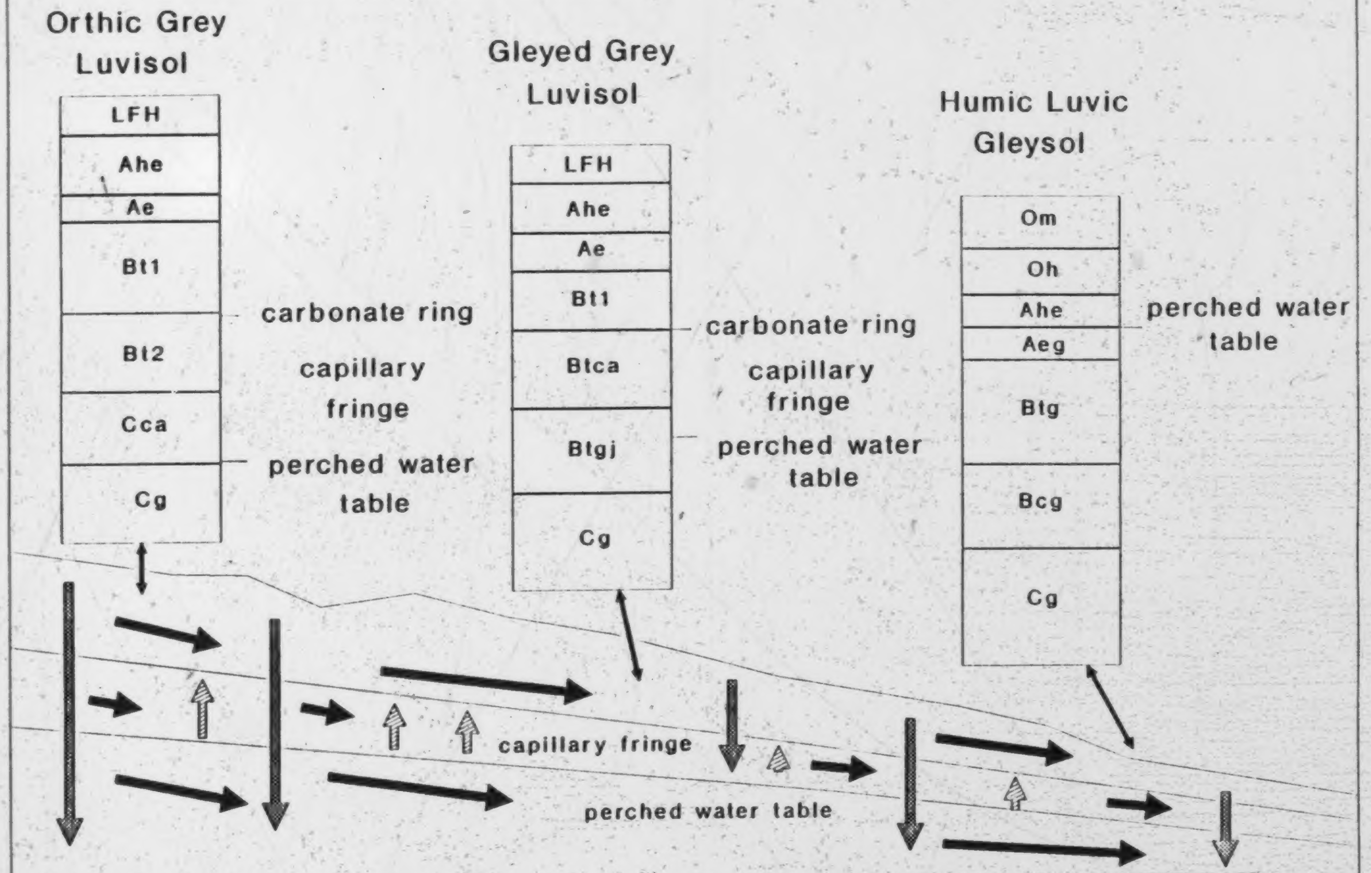

Orthic Grey Luvisol
LFH
Ahe
Ae
Bt1
Bt2
Cca
Cg
carbonate ring
capillary fringe
perched water table
Gleyed Grey Luvisol
LFH
Ahe
Ae
Bt1
Btca
Btgj
Cg
carbonate ring
capillary fringe
perched water table
Humic Luvic Gleysol
Om
Oh
Ahe
Aeg
Btg
Bcg
Cg
perched water table
capillary fringe
perched water table
Leaching
Lateral flow
Capillary rise

Figure 2.5 Conceptual illustration of catenary sequence at Ministik Research Station depicting soil profiles and water movement.

acid Ae and dense Bt horizons (Crown, 1977). The historical dominance of either grassland or forest vegetation types influences the resulting thickness of the Ah horizon. The thickness of the Ah horizon in turn determines the soils subgroup placement within the Luvisolic order of the Canadian System for Soil Classification. Removal of the forest vegetation by fire and subsequent succession from grassland back to forest have altered the physical and chemical composition of the surface horizons but the subsurface Bt remains (Crown, 1977).

Imperfectly drained Gleyed Grey Luvisol soils are found on lower slopes while poorly-drained Humic Luvic Gleysol soils occupy depressional and interridge areas (Bishoff, 1981). Very poorly drained Typic and Terric Mesisols occupy low lying and depressional areas that are often associated with surface drainage systems. These are the common soils of the catena. Intergrades, however, occur throughout.

Regionally the Cooking Lake Moraine is a recharge area. Its numerous depressions and low-lying areas, however, are subject to discharge of local or intermediate groundwater flow systems. The downward leaching of organic and inorganic compounds, coupled with the lateral flow of water downslope in association with the compact fine-textured nature of the glacial till substrate is responsible for the sequence of soils. Water entering the system infiltrates and moves downslope causing not only leaching but lateral translocation of suspended colloidal materials. This results in a finer texture of soil in the depressions. Water collects in the depressions and lower slope areas because the clayey till slows water percolation to the permanent water table. This results in the formation of perched water tables. The rising and lowering of the perched water table is caused by the relative balance between precipitation and slow percolation from perched water tables to permanent water tables.

2.5 Vegetation

The Cooking Lake area has been classified as an outlier of the Boreal Mixedwood forest zone (Rowe, 1972). Rowe's classification is based mainly on dominant tree species. Strong and Leggat (1981) classified the area as an island of Boreal Mixedwood within the Aspen Parkland. Their classification is based on soils, climate and vegetation data. Moss (1932) described the area as belonging to the poplar association of central Alberta while Bird (1961) considered it Aspen Parkland. This divergence of opinion is testimony to the dynamic and transitional nature of the entire system (Blyth and Hudson, 1987). The Cooking Lake area is therefore classified as ecotone between the Boreal Mixedwood forest to the north and the Aspen Parkland to the south (Zoltai, 1975; Reid, 1986; Blyth and Hudson, 1987). Common to all classifications, however, is the recognition of the aspen forest in various stages of succession as the dominant vegetation with some spruce and grassland in various combinations (Blyth and Hudson, 1987).

Large expanses of the Ministik area were dominated by white spruce (*Picea glauca* (Moench) Voss), the climatic climax species, until the 1890's when a large fire burned most of the area (Gates, 1980). Moss (1932) considers aspen (*Populus tremuloides* Michx.) to be the dominant species in the climax community on dry sites, with balsam poplar (*Populus balsamifera* L.) the dominant stage on moist sites where white spruce eventually dominates the climax community. Today, in the Ministik area, poplar forest is the most common vegetation type, with uplands dominated by aspen and imperfectly- to poorly-drained mineral soils dominated by balsam poplar. It is common to have both poplar species co-dominating a site.

Gates (1980) classified the vegetation of MWRS into five types: poplar forest, upland grassland, lowland grassland, willow and sedge meadows. The poplar forest is characterized by a dense understory of shrubs and herbs. The most common shrubs of the understory at MWRS are beaked hazelnut (*Corylus cornuta* Marsh.), wild rose (*Rosa acicularis* Lindl.), raspberry (*Rubus idaeus* L.), and saskatoon (*Amelanchier alnifolia* Nutt.) (Gates, 1980; Nietfeld, 1983).

Development of the upland grasslands at MWRS was influenced by the clearing and seeding of forest areas with agronomic species in the early 1900's. The native species have not yet replaced the agronomics. Gates (1980) found that bluegrass (*Poa pratensis* L.) and brome (*Bromus inermis* Leyss.) were the dominant grass species with clover (*Trifolium repens* L.), dandelion (*Taraxacum officinale* Weber) and strawberry (*Fragaria virginiana* Duchesne) being dominant forbs. Buckbrush (*Symphoricarpos occidentalis* Hook.) and wild rose often form a transition zone from the aspen forest to the upland grassland (Moss, 1932).

The willow habitat forms a band around the sedge meadows, representing a transition from the balsam poplar lowland forest. Sedges and marsh reed grass are the main understorey species of the willow habitat with salix spp. dominating the shrub layer (Gates, 1980). The wettest portions of the sedge fens are dominated by *Carex rostrata* Stokes, *Carex atherodes* Spreng., and *Carex aquatilis* Wahlenb., with marsh reed grass (*Calamagrostis canadensis*) dominating the drier fen areas (Bishoff, 1981). Emergent communities frame the areas around sloughs and lakes and may be dominated by *Scirpus validus* Vahl, *Typha latifolia* L., *Sparganium* spp., *Eleocharis palustris* (L.) R. & S., *Carex atherodes* and *Scholochloa festucacea* (Willd.) Link (Lewis et al, 1928; from; Bichlmaier, 1985).

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3.0 Vegetation Survey and Site Descriptions

3.1 Introduction

L. ochroleucus is an important forage species of Western Canada with its highest frequency of occurrence and per cent cover occurring in the *Populus*-dominated community types. These areas dominated by *Populus* species occur in regions described by Rowe (1972) as "Aspen Parkland", "Oak Aspen Parkland", "Boreal Mixedwood', and "Lower Foothills" which together occupy over 30% of the area of the prairie provinces. A vegetation survey of plant species distribution and abundance was conducted in order to identify plant communities in the study area at Ministik Wildlife Research Station (MWRS) in which *Lathyrus ochroleucus* (Hook) occurs. In plant community classification, a number of samples (stands) representing communities are grouped together based on shared characteristics into an abstract unit or class of plant communities (Whittaker, 1970). A cluster of species that repeatedly associate together require similar environmental conditions (Barbour et al., 1980). This repeated association of species is indirect evidence for strong interactions among them (Barbour et al., 1980). Each individual in a community interacts directly or indirectly with all other members of the community (Harper, 1977).

Floristic and soil differences among sites may contribute to varying growth rates of *Lathyrus ochroleucus*. If these differences among *L. ochroleucus* study sites are significant then the effect of these differences on its growth can be evaluated. In addition to determining the floristic differences among sites, the frequency and abundance of *L. ochroleucus* within the various community types within the study area at MWRS assisted in determining the importance of *the species* at the community level. Extrapolation from these results along with those from other studies allows the importance of *L. ochroleucus* to be evaluated on a regional scale.

3.1.1 Objectives

This study had four objectives:

1) To provide a plant community classification scheme within the study area that groups the vegetation sampling sites into plant community types;

2) To determine the importance of *L. ochroleucus* in the various communities identified in this plant community classification scheme;

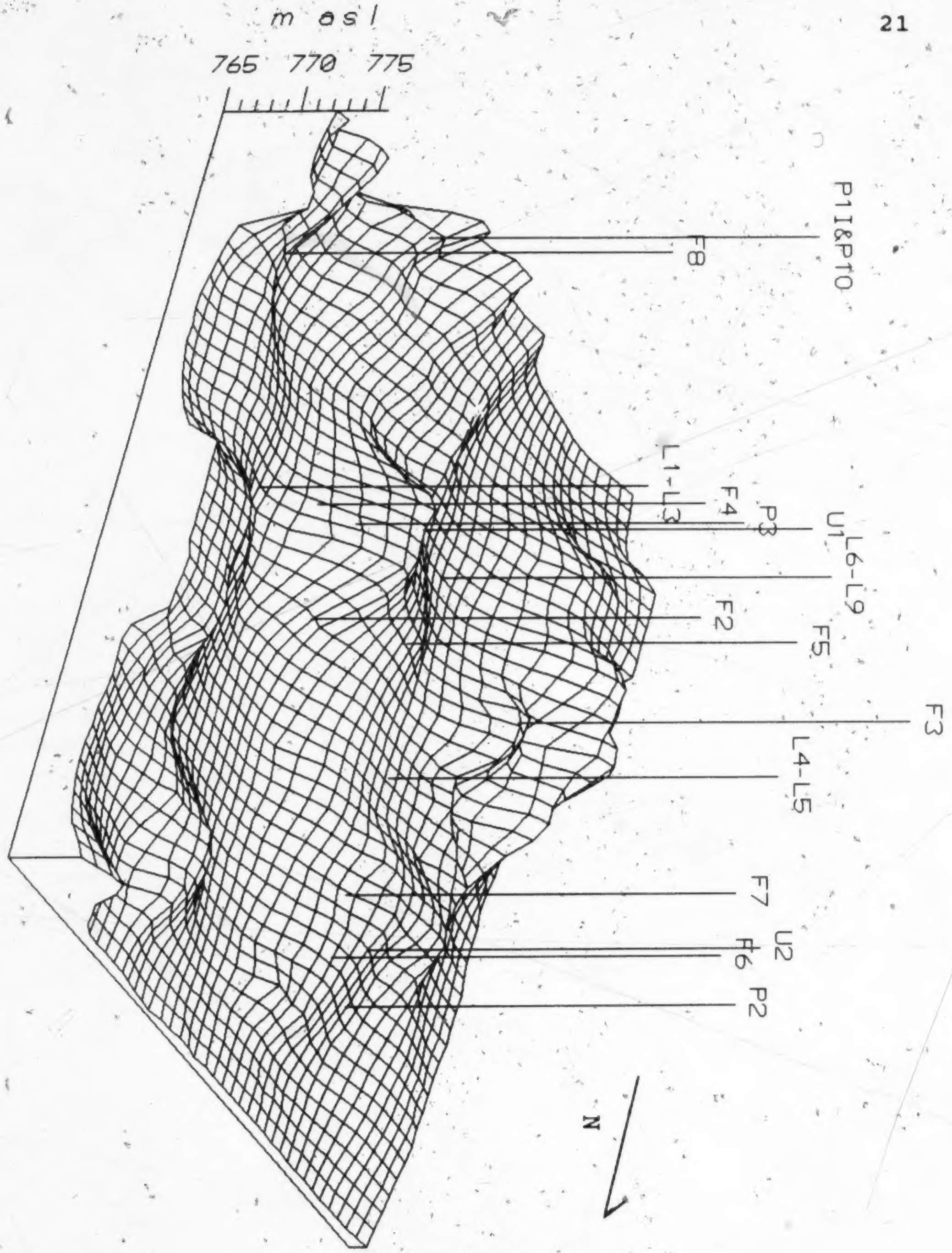
3) To determine the floristic similarity among the *L. ochroleucus* growth monitoring sites based on their placement in this plant community classification scheme;

4) To describe the characteristics of the *L. ochroleucus* height growth monitoring sites.

3.2 Methods

Field sampling methods involved the selection of 22 sampling sites based on subjective sampling criteria (Figure 3.1). Five sites were chosen because of their proximity to existing microclimate stations. Placement of the remaining 17 sites was based on visual inspection in an attempt to sample the diversity of study area plant communities. At each of the 22 sites a 1×1 m quadrat was randomly placed from four to six times. These sites were at a randomly-selected distance and orientation from the plot centre. Per cent cover of each species of shrub, forb, and graminoid within the quadrat was estimated visually. Additionally, the per cent cover of each tree species was visually estimated within a subjectively placed 10×10 m quadrat in each site.

Figure 3.1. Digital elevation model showing the location of plant community survey sites. The vertical exaggeration is ten times. The spacing of horizontal lines is ten meters. The letters F and P represent forest sites, L and U designate lowland and unforested upland sites respectively.


m asl
765 770 775
P1I&P10
F8
L1-L3
F4
P3
U1
L6-L9
F2
F5
F3
L4-L5
F7
U2
F6
P2
N

The average per cent cover for understorey species at each site was calculated from all 1×1 m quadrats. Tree species cover values were used directly.

Agglomerative hierarchical cluster analysis was used to perform a preliminary grouping of sites into communities. An examination of the results of this analysis assisted in determining the number of groups to request in Disjoint cluster analysis. Disjoint cluster analysis was performed on the vegetation data, and eight clusters were defined. Disjoint cluster analysis is a discrete clustering method that produces unique groups that have no overlap with other clusters (SAS Institute Inc., 1985). The observations (sites) are divided into clusters such that every observation belongs to one and only one cluster. This method uses Euclidean distances and was an effective method for finding clusters with a standard iterative algorithm for minimizing the sum of squared distances from the cluster means (SAS Institute Inc., 1985).

Discriminant analysis was used to evaluate the accuracy of the disjoint cluster analysis. This removed much of the subjectivity involved when establishing the number of groups and group membership. The discriminant function is based on minimizing the within group variance (pooled covariance) (SAS Institute Inc, 1985). Discriminant analysis has the potential to reclassify cluster analysis groupings by maximizing group differences and minimizing within group variance.

A Principal Components analysis ordination of the 22 stands was performed. Since the ordination used stands rather than species, the PCA was carried out on the covariance matrix (Gauch, 1982). Principal component analysis allows a multivariate data set, where each species is a dimension, to be represented by a few dimensions that account for a maximum of the variation. In addition a Detrended Correspondence analysis ordination of the 22 stands was preformed. Ordination techniques were used to arrange vegetation samples in a coordinate system so that distances between sample locations represent their similarity or dissimilarity.

L. ochroleucus growth monitoring sites were described in terms of soils and site characteristics. The soil descriptions follow the methodology outlined by the Expert Committee on Soil Survey (1983). The soils were classified according to the Canadian System of Soil Classification (Canadian Soil Survey Committee, 1978).

3.3 RESULTS

Eight distinct plant community types were identified by disjoint cluster analysis. When the disjoint cluster analysis groupings were analyzed using discriminant analysis, the overall correct classification accuracy was 91.3%. This was because two out of the 22 sites were "mis-classified" by disjoint cluster analysis according to the linear discriminant function. Both "mis-classified" sites were in groups by themselves. They were reclassified by the linear discriminant function into an existing group, so the number of clusters (plant community types) dropped from eight to six. The clumping of sites in euclidean space as defined by the first and second principal components is in accordance with the community types identified by cluster and discriminant analysis (Figure 3.2). The first and second principal components from the principal component analysis of the 22 sites accounted for 40% and 18%, respectively, of the variation contained in the original variables (species per cent cover). Of the six plant community types, two were forested (Table 3.1, 3.2), one was unforested upland (Table 3.3), and three were wetland plant community types (Table 3.4, 3.5, 3.6).

One forest community was dominated by *Populus tremuloides* (Table 3.1) and the other by *Populus balsamifera* (Table 3.2). *Corylus cornuta, Rubus idaeus* and *Rosa acicularis* dominated the shrub layer in both forest community types, however, their per cent cover values were higher in the *Populus tremuloides*-dominated community. *Aralia nudicaulis*

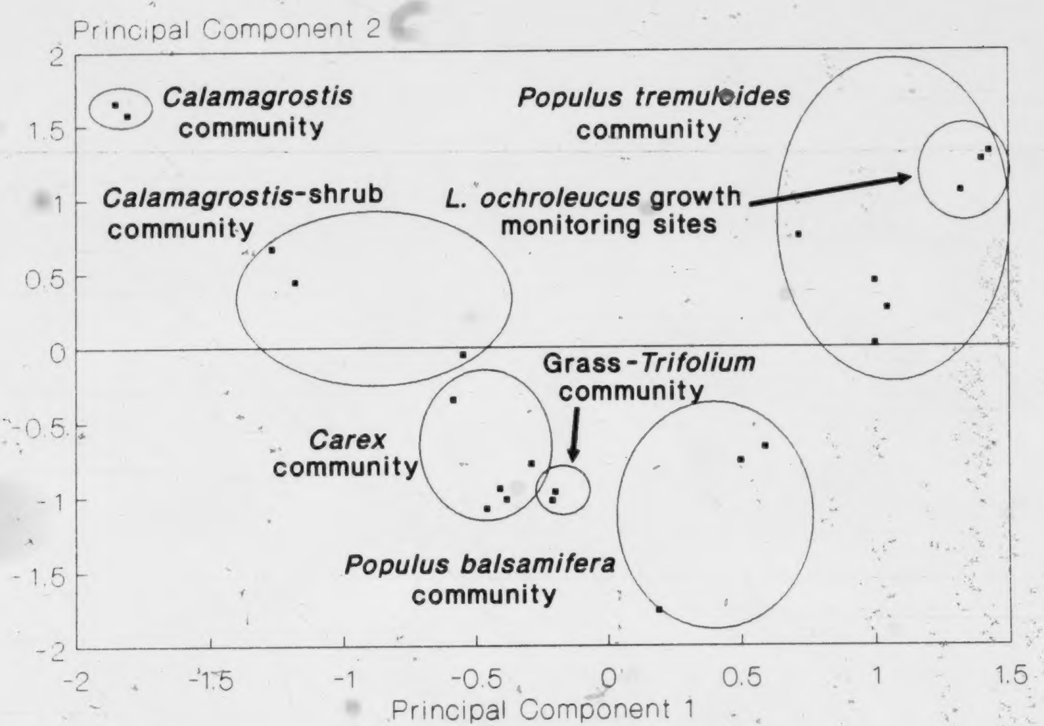


Figure 3.2 Principal component ordination of plant community sampling sites, MWRS. The circles enclose the site groupings as defined by cluster and discriminant analysis.

dominated the forb layer in both community types. Although both community types had many of the herbaceous species in common they also had species which were unique to each (Table 3.1, 3.2). The *Populus balsamifera*-dominated community type had more species in common with the moist lowland community types. These included: *Cirsium arvensis, Urtica gracilis, Gentianella amarella, Stachys palustris, Mentha arvensis* and *Equisetum* spp. The total mean per cent cover was greater in the *Populus termuloides*-dominated community due largely to its higher abundance of shrubs, although this trend was not tested statistically.

The Grass-*Trifolium repens*-dominated community type had *Rubus idaeus, Populus tremuloides (< 4 m high), Rosa acicularis* and *Symphoricarpos occidentalis* as the dominant shrubs, although their cover was sparse (< 13%, Table 3.3). The dominant forbs included *Trifolium repens, Cirsium arvense*, and *Taraxacum officinale*. In addition, there was a variety of upland grasses, with *Bromus inermis* one of the dominants (Table 3.3).

The three plant community types of the wetland areas can be referred to as: the *Calamagrostis canadensis*-dominated plant community, the *Calamagrostis*-Shrub plant community and the *Carex* plant community. Many of the plant species in these community types are similar, but, species cover values varied among them. The *Calamagrostis canadensis*-dominated plant community type was dominated by an almost continuous layer of *Calamagrostis canadensis* with *Cirsium arvense, Polygonum amphibium*, and *Scutellaria galericulata* being important forbs (Table 3.4). The *Calamagrostis*-Shrub community had two phases, both dominated by an abundance of *Calamagrostis canadensis*. The phases were separated based on the dominant shrubs. One phase was dominated by *Salix* species and the other by *Rubus idaeus*. The *Carex atherodes/C. rostrata*-dominated plant community type had *Salix* spp. as the dominant shrubs, and *Polygonum amphibium, Petasites sagittatus* and *Potentilla palustris* were the most abundant forbs (Table 3.4).

Table 3.1 ***Populus tremuloides*****-dominated plant community type**

PLANT SPECIES	PER CENT COVER (n=7)		
TREE LAYER	MEAN	MAX	MIN
Populus tremuloides	*56.4*	*70.0*	*44.2*
Populus balsamifera	*11.7*	*33.2*	*0.0*
Total	68.1		
SHRUB LAYER			
Corylus cornuta	*16.4*	*35.3*	*1.0*
Rubus idaeus	*13.8*	*30.3*	*1.4*
Rosa acicularis	*7.9*	*25.8*	*1.4*
Amelanchier alnifolia	*1.8*	*3.2*	*0.5*
Symphoricarpus occidentalis	*1.7*	*2.5*	*1.1*
Populus tremuloides	*1.4*	*3.7*	*0.0*
Cornus stolonifera	*1.1*	*4.0*	*0.0*
Viburnum edule	*0.6*	*2.5*	*0.0*
Symphoricarpus albus	*0.5*	*1.5*	*0.0*
Shepherdia canadensis	*0.3*	*2.2*	*0.0*
Lonicera involucrata	*0.3*	*1.2*	*0.0*
Ribes oxyacanthoides	*0.2*	*0.7*	*0.0*
Lonicera dioica	*0.2*	*0.5*	*0.0*
Populus balsamifera	*0.1*	*0.3*	*0.0*
Prunus pensylvanica	*0.0*	*0.2*	*0.0*
Ribes hudsonianum	*0.0*	*0.2*	*0.0*
Total	46.3		
FORB LAYER			
Forbs			
Aralia nudicaulis	*13.7*	*27.3*	*1.5*
Rubus pubescens	*3.6*	*5.7*	*0.3*
Aster ciliolatus	*3.0*	*5.0*	*1.8*
Cornus canadensis	*1.8*	*2.7*	*0.0*
Lathyrus ochroleucus	*1.7*	*5.2*	*0.3*
Fragaria virginana	*1.5*	*2.0*	*0.9*
Galium boreale	*1.3*	*2.6*	*0.5*
Disporum trachycarpum	*1.0*	*2.3*	*0.2*
Galium triflorum	*1.0*	*2.2*	*0.3*
Aster conspicuus	*0.9*	*2.2*	*0.0*
Vicia americana	*0.7*	*2.2*	*0.0*
Petasites palmatus	*0.5*	*1.5*	*0.0*
Orthilia secunda	*0.5*	*1.3*	*0.0*
Maiantheum canadense	*0.5*	*0.8*	*0.0*
Mertensia paniculata	*0.4*	*1.8*	*0.0*
Viola renifolia	*0.4*	*1.0*	*0.1*
Lathyrus venosus	*0.2*	*1.7*	*0.0*
Linnaea borealis	*0.2*	*0.7*	*0.0*
Actaea rubra	*0.2*	*0.4*	*0.0*
Mitella nuda	*0.2*	*0.8*	*0.0*
Heracleum lanatrum	*0.2*	*0.9*	*0.0*
Traxacum officinale	*0.1*	*0.6*	*0.0*
Geum allepicum	*0.1*	*0.3*	*0.0*
Pyrola asarifolia	*0.1*	*0.2*	*0.0*
Osmorhiza depauperata	*0.0*	*0.2*	*0.0*
Galeopsis tetrahit	*0.0*	*0.2*	*0.0*
Achillea millefolium	*0.0*	*0.2*	*0.0*
Viola regulosa	*0.0*	*0.1*	*0.0*
Sonchus arvensis	*0.0*	*0.1*	*0.0*
Total	45.5		
Grasses			
Calamagrostis canadensis	*2.0*	*11.3*	*0.1*
Agropyron subsecundum	*1.0*	*4.5*	*0.0*
Total	3.0		

Total mean cover 162.9

Table 3.2 *Populus balsamifera*-dominated plant community type

PLANT SPECIES	PERCENT COVER (n=3)		
TREE LAYER	MEAN	MAX	MIN
Populus balsamifera	52.6	76.7	39.4
Populus tremuloides	11.8	20.0	0.0
Total	64.4		
SHRUB LAYER			
Corylus cornuta	12.7	23.0	0.0
Rubus idaeus	10.7	19.2	0.0
Rosa acicularis	3.8	9.8	0.7
Symphoricarpus occidentalis	1.4	2.6	0.2
Populus tremuloides	1.0	3.0	0.0
Amelanchier alnifolia	0.9	2.4	0.0
Cornus stolonifera	0.8	1.4	0.0
Lonicera involucrata	0.8	2.0	0.0
Viburnum edule	0.4	1.0	0.0
Prunus pensylvanica	0.3	1.0	0.0
Lonicera dioica	0.3	0.8	0.0
Ribes oxyacanthoides	0.1	0.3	0.0
Symphoricarpus albus	0.0	0.1	0.0
Total	32.1		
FORB LAYER			
Forbs			
Aralia nudicaulis	5.2	8.0	0.0
Cirsium arvense	3.7	11.2	0.0
Aster ciliolatus	2.2	3.7	0.2
Rubus pubescens	1.8	2.7	0.3
Fragaria virginiana	1.2	2.6	0.3
Cornus canadensis	0.9	1.6	0.0
Galeopsis tetrahit	0.9	1.6	0.0
Heracleum lanatum	0.8	2.3	0.0
Equisetum arvense	0.8	2.3	0.0
Lathyrus ochroleucus	0.7	1.2	0.3
Petasites palmatus	0.7	2.0	0.0
Urtica gracilis	0.6	1.7	0.0
Galium boreale	0.4	1.0	0.0
Actaea rubra	0.4	1.3	0.0
Mitella nuda	0.4	1.2	0.0
Galium triflorum	0.4	1.1	0.0
Gentianella amarella	0.3	1.0	0.0
Disporum trachycarpum	0.3	0.7	0.0
Stachys palustris	0.3	0.8	0.0
Viola regulosa	0.3	0.8	0.0
Maianthemum canadense	0.2	0.5	0.0
Vicia americana	0.2	0.4	0.0
Mentha arvensis	0.2	0.5	0.0
Viola renifolia	0.2	0.5	0.0
Taraxacum officinale	0.1	0.2	0.0
Linnaea borealis	0.1	0.2	0.0
Pyrola asarifolia	0.1	0.2	0.0
Lathyrus venosus	0.1	0.2	0.0
Equisetum pratense	0.1	0.2	0.0
Trifolium repens	0.1	0.2	0.0
Orthilia secunda	0.0	0.1	0.0
Total	23.2		
Grasses			
Calamagrostis canadensis	2.0	4.9	0.2
Agropyron subsecundum	0.1	0.2	0.0
Total	2.1		

Total mean cover 121.8

Table 3.3 Grass-*Trifolium repens*-dominated community type

PLANT SPECIES	PERCENT COVER (n=2)		
SHRUB LAYER	MEAN	MAX	MIN
Rubus idaeus	*3.7*	*4.2*	*3.2*
Populus tremuloides	*3.2*	*5.3*	*1.0*
Rosa acicularis	*2.3*	*2.3*	*2.3*
Symphoricarpus occidentalis	*1.8*	*3.0*	*0.7*
Populus balsamifera	*0.5*	*1.0*	*0.0*
Ribes oxyacanthoides	*0.3*	*0.5*	*0.0*
Amelanchier alnifolia	*0.1*	*0.2*	*0.0*
Betula papyrifera	*0.1*	*0.2*	*0.0*
Corylus cornuta	*0.1*	*0.2*	*0.0*
Total	12.1		
FORB LAYER			
Forbs			
Trifolium repens	*20.8*	*30.7*	*10.8*
Cirsium arvense	*7.5*	*11.7*	*3.3*
Traxacum officinale	*6.8*	*12.2*	*1.3*
Galium boreale	*5.8*	*11.5*	*0.0*
Solidago gigantea	*4.7*	*9.3*	*0.0*
Aster ciliolatus	*1.8*	*2.3*	*1.3*
Agrimonia striata	*1.3*	*2.5*	*0.0*
Fragaria virginiana	*1.0*	*1.3*	*0.7*
Lathyrus ochroleucus	*0.3*	*0.7*	*0.0*
Achillea millefolium	*0.3*	*0.5*	*0.2*
Solidago canadensis	*0.3*	*0.7*	*0.0*
Plantago major	*0.3*	*0.5*	*0.0*
Geum aleppicum	*0.3*	*0.5*	*0.0*
Vicia americana	*0.3*	*0.3*	*0.2*
Anemone canadensis	*0.2*	*0.3*	*0.0*
Cornus canadensis	*0.1*	*0.2*	*0.0*
Gentianella amarella	*0.1*	*0.2*	*0.0*
Viola renifolia	*0.1*	*0.2*	*0.0*
Petasites palmatus	*0.1*	*0.2*	*0.0*
Total	51.11		
Grasses			
Grass spp. (upland)	27.3	39.7	15.0
Bromus inermis	*3.5*	*7.0*	*0.0*
Agropyron subsecundum	*1.5*	*3.0*	*0.0*
Total	32.3		
Total mean cover	95.5		

Table 3.4 ***Calamagrostis canadensis*****-dominated community type**

PLANT SPECIES		PERCENT COVER (n=2)		
SHRUB LAYER		MEAN	MAX	MIN
Salix spp.		*6.3*	*8.5*	*4.2*
Ribes hudsonianum		*0.1*	*0.3*	*0.0*
Ribes oxyacanthoides		*0.1*	*0.3*	*0.0*
	Total	6.5		
FORB LAYER				
Forbs				
Cirsium arvense		*4.8*	*9.5*	*0.0*
Polygonum amphibium		*2.5*	*4.2*	*0.8*
Scutellaria galericulata		*1.2*	*1.7*	*0.8*
Urtica gracilis		*0.8*	*1.5*	*0.0*
Mentha arvensis		*0.8*	*1.5*	*0.0*
Galeopsis tetrahit		*0.5*	*0.5*	*0.5*
Petasites sagittatus		*0.5*	*1.0*	*0.0*
Potentilla palustris		*0.4*	*0.8*	*0.0*
Equisetum arvense		*0.2*	*0.3*	*0.0*
Sium suave		*0.1*	*0.3*	*0.0*
	Total	11.5		
Grasses				
Calamagrostis canadensis		*88.8*	*89.8*	*87.8*
	Total	88.8		
Sedges				
Carex atherodes		*0.2*	*0.3*	*0.0*
	Total	0.2		
	Total mean cover	107.0		

Table 3.5 *Calamagrostis*/Shrub-dominated community type

PLANT SPECIES	PERCENT COVER (n=3)		
SHRUB LAYER	MEAN	MAX	MIN
Shrubs			
Salix spp.	*21.8*	*45.0*	*0.5*
Rubus idaeus	*10.4*	*30.3*	*0.0*
Populus tremuloides	*3.4*	*10.3*	*0.0*
Rosa acicularis	*2.4*	*7.3*	*0.0*
Populus balsamifera	*0.5*	*1.5*	*0.0*
Prunus pensylvanica	*0.3*	*0.8*	*0.0*
Lonicera involucrata	*0.2*	*0.7*	*0.0*
Ribes hudsonianum	*0.1*	*0.3*	*0.0*
Ribes lacustre	*0.1*	*0.3*	*0.0*
Total	39.2		
FORB LAYER			
Forbs			
Polygonum amphibium	*2.1*	*4.7*	*0.0*
Petasites sagittatus	*2.0*	*6.0*	*0.0*
Cornus canadensis	*1.2*	*1.7*	*0.5*
Cirsium arvense	*1.2*	*3.5*	*0.0*
Symphoricarpus occidentalis	*0.8*	*2.5*	*0.0*
Viola regulosa	*0.7*	*2.2*	*0.0*
Vicia americana	*0.7*	*2.2*	*0.0*
Agrimonia striata	*0.6*	*1.8*	*0.0*
Galium boreale	*0.5*	*1.5*	*0.0*
Heracleum lanatum	*0.4*	*1.3*	*0.0*
Fragaria virginiana	*0.4*	*1.2*	*0.0*
Lathyrus ochroleucus	*0.4*	*1.2*	*0.0*
Urtica gracilis	*0.3*	*1.0*	*0.0*
Taraxacum officinale	*0.3*	*0.8*	*0.0*
Mentha arvensis	*0.3*	*0.5*	*0.0*
Galeopsis tetrahit	*0.3*	*0.5*	*0.0*
Aster puniceus	*0.2*	*0.7*	*0.0*
Aster ciliolatus	*0.2*	*0.7*	*0.0*
Achillea millefolium	*0.2*	*0.5*	*0.0*
Equisetum arvense	*0.1*	*0.3*	*0.0*
Potentilla palustris	*0.1*	*0.3*	*0.0*
Rubus pubescens	*0.1*	*0.3*	*0.0*
Scutellaria galericulata	*0.1*	*0.3*	*0.0*
Galium triflorum	*0.1*	*0.3*	*0.0*
Maianthemum canadense	*0.1*	*0.3*	*0.0*
Stellaria longifolia	*0.1*	*0.3*	*0.0*
Anemone canadensis	*0.1*	*0.2*	*0.0*
Geum aleppicum	*0.1*	*0.2*	*0.0*
Aralia nudicaulis	*0.1*	*0.2*	*0.0*
Stachys palustris	*0.1*	*0.2*	*0.0*
Total	13.9		
Grasses			
Calamagrostis canadensis	*40.6*	*53.3*	*26.0*
Agropyron subsecundum	*0.6*	*1.8*	*0.0*
Grass spp.	*0.4*	*1.3*	*0.0*
Phleum pratense	*0.1*	*0.2*	*0.0*
Total	41.6		
Sedges			
Carex rostrata	*2.2*	*6.7*	*0.0*
Carex spp.	*0.4*	*1.3*	*0.0*
Total	2.6		
Total mean cover	97.4		

Table 3.6 *Carex atherodes/C. rostrata*-dominated community type

PLANT SPECIES	PERCENT COVER (n=5)		
SHRUB LAYER	MEAN	MAX	MIN
Salix spp.	*8.9*	*29.0*	*0.0*
Betula papyrifera	*3.2*	*8.5*	*0.0*
Ribes hudsonianum	*0.7*	*3.6*	*0.0*
Lonicera involucrata	*0.3*	*1.3*	*0.0*
Ribes oxyacanthoides	*0.2*	*1.0*	*0.0*
Populus balsamifera	*0.1*	*0.4*	*0.0*
Total	13.4		
FORB LAYER			
Forbs			
Polygonum amphibium	*4.3*	*8.6*	*0.5*
Petasites sagittatus	*2.1*	*6.4*	*0.0*
Potentilla palustris	*1.8*	*4.8*	*0.0*
Scutellaria galericulata	*0.9*	*2.5*	*0.0*
Mentha arvensis	*0.8*	*2.0*	*0.0*
Urtica gracilis	*0.8*	*3.5*	*0.0*
Cicuta maculata	*0.8*	*3.0*	*0.0*
Stellaria longifolia	*0.7*	*1.6*	*0.0*
Equisetum fluvatile	*0.5*	*1.3*	*0.0*
Galeopsis tetrahit	*0.5*	*1.3*	*0.0*
Aster puniceus	*0.5*	*2.0*	*0.0*
Geum aleppicum	*0.3*	*0.8*	*0.0*
Equisetum arvense	*0.3*	*0.8*	*0.0*
Sium suave	*0.2*	*0.5*	*0.0*
Cornus canadensis	*0.1*	*0.4*	*0.0*
Bidens cernua	*0.1*	*0.4*	*0.0*
Fragaria virginana	*0.1*	*0.3*	*0.0*
Taraxacum officinale	*0.0*	*0.2*	*0.0*
Galium triflorum	*0.0*	*0.2*	*0.0*
Total	14.8		
Grasses			
Glyceria grandis	*12.8*	*63.0*	*0.0*
Calamagrostis canadensis	*6.6*	*17.5*	*0.0*
other	*4.0*	*10.0*	*1.0*
Total	23.4		
Sedges			
Carex atherodes	*15.4*	*72.5*	*0.0*
Carex rostrata	*10.7*	*38.3*	*0.0*
Carex aquatilis	*7.6*	*25.0*	*0.0*
Carex spp.	*0.9*	*2.4*	*0.0*
Juncus balticus	*0.1*	*0.6*	*0.0*
Total	34.7		
Total mean cover	86.4		

Detrended correspondence analysis ordination was more sucessful than PCA ordination in relating community variation to complex environmental gradients. The first axis in the DCA ordination represents a complex environmental gradient involving changes in topographic position and soil moisture regime (Figure 3.3). The *Populus*-dominated and Grass-*Trifolium repens*-dominated community types were found in the drier topographic positions such as knoll apexes and upper and mid slope positions (Figure 3.3). The depressions and lower slope areas were dominated by wetland community types (Figure 3.3). *L. ochroleucus* had its greatest frequency of occurence (100%) and highest per cent cover in the *Populus*-dominated community types.

The three *L. ochroleucus* growth monitoring sites were similar floristically. All growth monitoring sites were classified into the *Populus tremuloides*-dominated community based on similar vegetation characteristics as determined by cluster and discriminant analysis. Within the *Populus tremuloides*-dominated community the three *L. ochroleucus* growth monitoring sites were more similar than other sites classified into the community. This can be seen by their grouping in the upper right corner of the plant community ordination diagram (Figure 3.2).

The *L. ochroleucus* growth monitoring sites had similar soils but had differences in aspect, slope and site position (Appendix I). The soils of the three *L. ochroleucus* growth monitoring sites were similar with respect to horizon sequence, depth, colour, pH and texture (Appendix I). The soils at all three sites were classified as Orthic Grey Luvisols and fell within the limits of the Cooking Lake soil series.

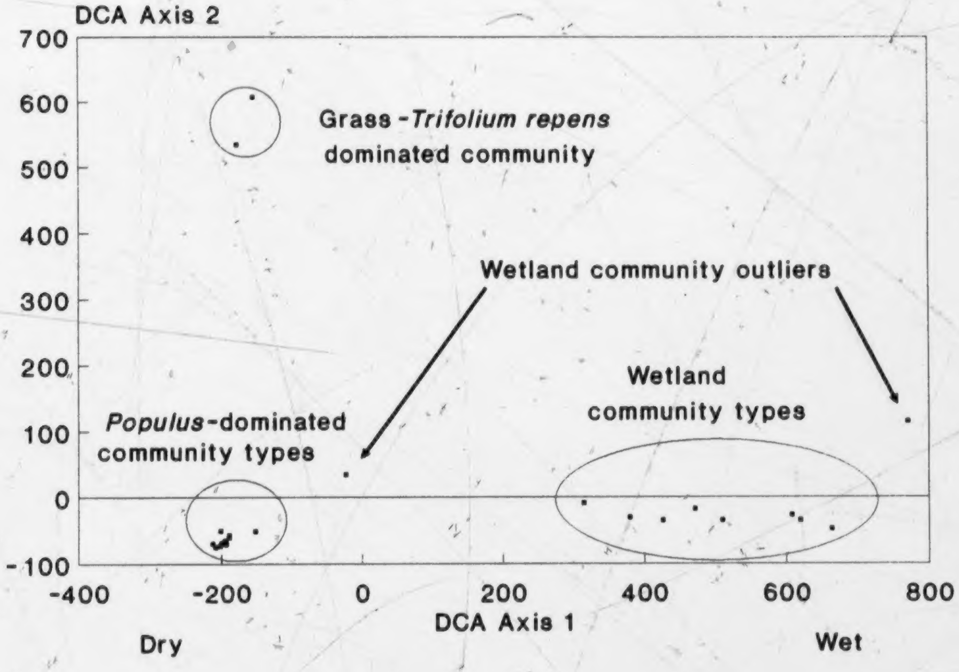


Figure 3.3 Detrended correspondence analysis (DCA) ordination of plant community sampling sites, MWRS. DCA axis 1 represents a complex environmental gradient involving changes in topographic position and soil moisture regime.

3.4 DISCUSSION

3.4.1 ORDINATION

Detrended correspondence analysis (DCA) ordination was more sucessful than PCA ordination in relating community variation to complex environmental gradients. On the other hand, PCA ordination appeared to provide better insight into community structure as indicated by the close association between the cluster analysis groupings and the distribution of sites in euclidean space as defined by PCA ordination (Figure 3.2). The first axis in the DCA ordination represents a complex environmental gradient involving changes in topographic position and soil moisture regime (Figure 3.3). The distribution of communities along the moisture gradient, however, was not well defined. There were three major groupings, the *Populus*-dominated community types, the Grass-*Trifolium repens*-dominated community type and the wetland community types (Figure 3.3). The plant community types can be arranged along a soil catena which illustrates the relationship between topography, soils, and vegetation (Figure 3.4). Discussion is based on the communities identified by the community classification scheme and displayed in the PCA ordination.

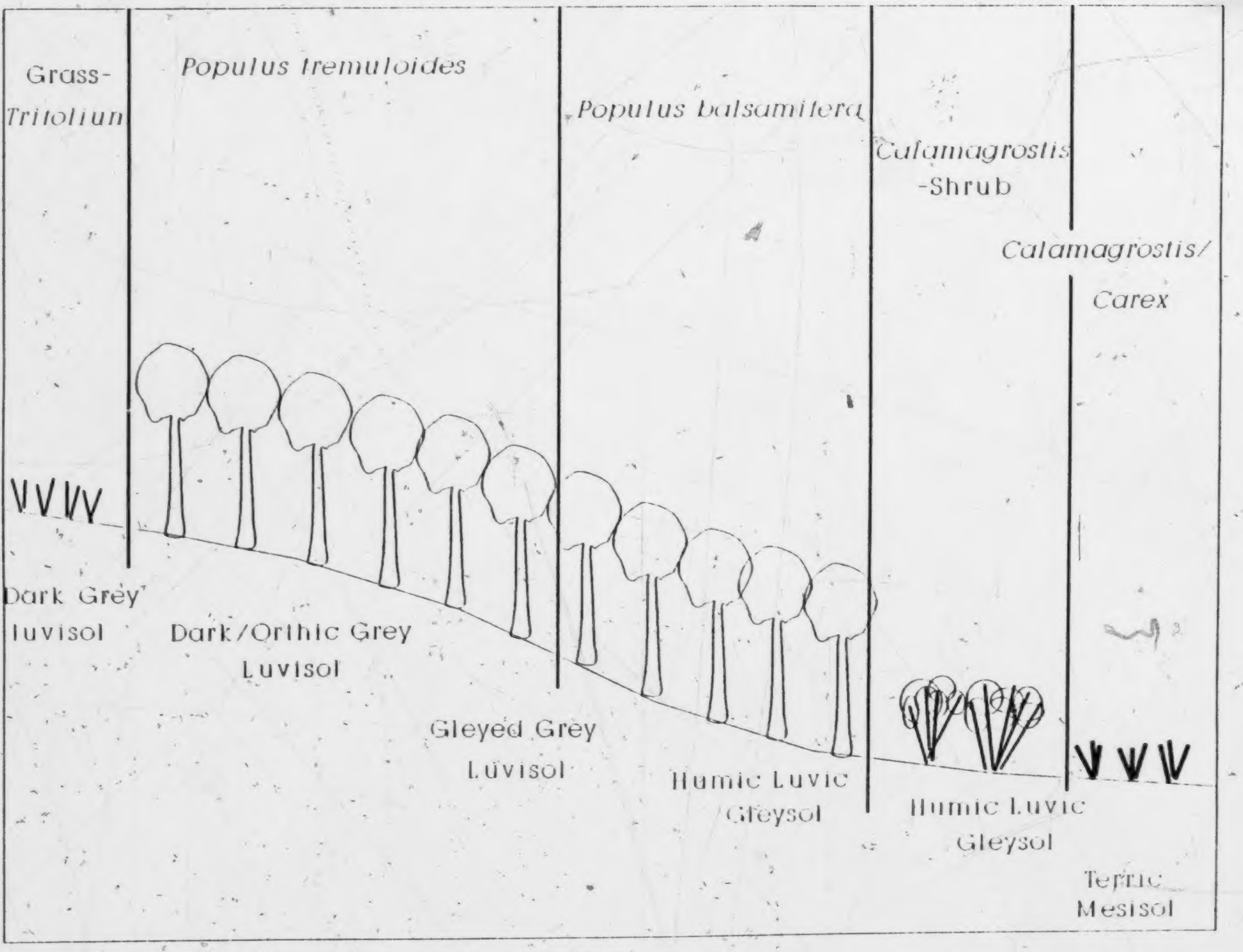
3.4.2 *Populus tremuloides* and *Populus balsamifera*-dominated community types.

The *Populus tremuloides* and *Populus balsamifera*-dominated community types were similar to the communities described for central Alberta by Moss (1932). He described the poplar consociation where *Populus tremuloides* was the climax tree on drier and more southerly parts of the region. *Populus balsamifera* was the subclimax tree (*Picea glauca* being climax) of the poplar consociation on the more moist sites, especially in the northern and western parts of the region (Moss (1932). It has since been recognized that on the Cooking Lake Morraine, succession to mature spruce forest is never reached (Polster and Watson, 1979). Reid (1964), after studying the reason for lack of spruce at Elk

Island National Park (approx. 30 km north of MWRS), concluded that bison were retarding succession from aspen to spruce forest by rubbing and subsequently killing young spruce. The presence of bison may partly explain the lack of spruce at MWRS where many spruce saplings have been killed and smaller trees severely damaged.

Populus tremuloides was found in the drier upper slope positions while *Populus balsamifera* was found in the middle and lower slope positions (Figure 3.4). Both the *P. tremuloides*- and *P. balsamifera*-dominated community types had distinctive tree, shrub, and forb layers. However, the shrubs were not separated into different strata as other researchers have done (Moss, 1932; Sheffler, 1976; Bishoff, 1981). The dominant shrubs in both poplar community types, in order of abundance, were *Corylus cornuta, Rubus idaeus*, and *Rosa acicularis*, which is reported by other researchers. Moss (1932) found that for the aspen consociation, *Rosa acicularis* and *Rubus idaeus* were the co-dominant shrubs, while Sheffler (1979) reported *Symphoricarpos occidentalis* and *Rosa acicularis*, and Bishoff (1981) reported *Rosa acicularis* and *Corylus cornuta*. Blyth and Hudson (1987) found that, in Elk Island National Park, *Corylus cornuta* dominated the open poplar forest comprising 20-30% of the live stems. *Rosa acicularis* was the next most prevalent shrub in terms of live stems. The per cent cover of shrubs in the *Populus tremuloides*-dominated community (46.3%) was higher than in the *Populus balsamifera*-dominated community (32.1%), although this trend was not tested statistically. This is consistent with the results reported by Hardy and Associates (1986) for similar communities in Elk Island National Park (EINP), though their shrub ground cover values were approximately 30% higher. This discrepancy in cover values could be due to more intensive utilization of browse in the study area at MWRS than occurred in EINP. Milner (1977) reported that in areas subjected to browsing, stem density was reduced, and the shrubs were shorter and had a fewer number of twigs. Although EINP, has higher ungulate densities than MWRS, the study area at MWRS was a favourite gathering place for

Figure 3.4 Plant communities along a soil catena at Ministik Wildlife Research Station. Notice the relationship between topography, soils, and vegetation.


Grass-
Trifolium
Populus tremuloides
Populus balsamifera
Calamagrostis
-Shrub
Calamagrostis/
Carex
Dark Grey
luvisol
Dark/Orthic Grey
Luvisol
Gleyed Grey
Luvisol
Humic Luvic
Gleysol
Humic Luvic
Gleysol
Terric
Mesisol

bison which could explain the heavy browse utilization in this area.

The dominant herbaceous species of the *P. tremuloides* and *P. balsamifera* dominated community types are similar to those reported by other researchers (Moss 1932; Lynch 1955; Bird 1961; Sheffler 1976, Bishoff 1981; Hardy and Associates, 1986). In this study, *Aralia nudicaulis* was the dominant forb in both of the poplar-dominated community types. It had higher cover values in the *P. tremuloides*-dominated community, however, this trend was not statistically tested. Hardy and Associates (1986) reported that *Aralia nudicaulis* was the dominant forb in their aspen/beaked hazel/wild sarsparilla, aspen/balsam poplar, and balsam poplar/beaked hazel/wild sarsparilla community types at Elk Island National Park. Bishoff (1981) also found *Aralia nudicaulis* was the most distinctive species in the forest community at Elk Island National Park. Blyth and Hudson (1987) reported that in many areas where the aspen forest has a crown closure of 70 to 100% the hazel and rose shrubs may be almost absent and replaced by *Aralia nudicaulis* or *Calamagrostis spp.*

The *Populus balsamifera*-dominated community type has species in common with the moist lowland community types which were not found in the *P. tremuloides*-dominated community. These include: *Cirsium arvensis, Urtica gracilis, Gentianella amarella, Stachys palustris, Mentha arvensis* and *Equisetum* spp. Of the seven herbaceous species listed by Moss (1932) as characteristic of the balsam poplar consociation four had higher cover values in the *P. balsamifera*-dominated community than in the *P. tremuloides*-dominated community type. Similarly, the four species listed as characteristic of the aspen consociation all had higher cover values in the *P. tremuloides*-dominated community type except *Schizachne purpurascens,* which was not found in this study.

3.4.3 Grass-*Trifolium repens*-dominated community type

The Grass-*Trifolium repens*-dominated community type (G-Tr.) developed as a result of the clearing and seeding of forest areas with agronomic species in the 1940's (Kershaw, per. com.). They are found in the upper and middle slope positions where the forest vegetation has been removed or disturbed (Figure 3.3). Before cultivation, localized areas of native grassland were maintained by fire which was set largely by Indians (Bird, 1961). These native grasslands were dominated by *Festuca scabrella, Stipa spartea,* and *Koeleria cristata* (Bird, 1961). The native species have not replaced the more competitive agronomics. The G-Tr. community is dominated by forbs such as *Trifolium repens, Cirsium arvense, Taraxacum officinale,* and *Galium boreale* as well as agronomic graminoids, including *Bromus inermis* L. Gates (1980) reported similar findings with *Poa pratensis* L. and *Bromus inermis* the dominant grass species and *Trifolium repens, Taraxacum officinale,* and *Fragaria virginiana* being the dominant forbs. Hardy and Associates (1986) identified two grassland communities typical of Elk Island National Park, dominated by either *Poa pratensis* and/or *Bromus inermis,* with important forbs being *Achillea millefolium, Aster laevis, and Solidago* spp.

Species including *Rubus idaeus, Populus tremuloides, Rosa acicularis,* and *Symphoricarpus occidentalis* dominated the sparse shrub layer in the G-Tr. community. A predominance of these woody species suggests an invasion of what was once grassland, with *P. tremuloides* providing the direct evidence of succession towards aspen forest. *Symphoricarpus occidentalis, Rosa acicularis, Rubus spp., Epilobium angustifolium, Aster spp., Solidago spp., Agropyron spp., Bromus spp.,* and *Calamagrostis canadensis* are the characteristic species of these seral stages in succession from grassland to aspen forest communities (Moss, 1932). *Symphoricarpus occidentalis* is characteristic of the zone between grassland and aspen forest (Pettapeice, 1969; Bailey and Wroe, 1974; Sheffler, 1976; Wheeler, 1976). The presence of these seral communities in the natural succession from grassland to aspen forest may be maintained indefinitely by grazing and browsing (Moss, 1932; Lynch, 1955; Bird, 1961, Bishoff, 1981). This appears to be the case at MWRS where the G-Tr. community type is a seral stage between grassland and aspen forest which is maintained in a dynamic but intermediate successional stage by the grazing and browsing of the native ungulate population.

3.4.4 Wetland Community Types

Conceptually, the wetland communities can be thought of as being arranged along a moisture gradient. Areas that are influenced by different moisture regimes exhibit differences in species abundance and composition. Jeglum (1972) reported moisture and nutrients to be more important than disturbance in influencing wetlands in the boreal forest in Saskatchewan. Similarly, Walker and Coupland (1968) found that the distribution of herbaceous species in Saskatchewan sloughs was strongly influenced by water regime. The *Carex atherodes/C. rostrata*-dominated community type is found in the wettest areas (Figure 3.4). Where the soils are drier, *Carex* species were replaced by *Calamagrostis canadensis* and the *Calamagrostis canadensis* community type dominated. Where the *Carex atherodes/C. rostrata*-dominated community type appeared to be disturbed by bison trails, community dominance favoured *Glyceria grandis*. In some areas where *Salix* species dominated the shrub layer, microscale relief allowed for a greater diversity of moisture conditions and thus species assemblages. These areas were dominated by the *Salix* phase of the *Calamagrostis*-Shrub community type. The *Rubus idaeus* phase of the *Calamagrostis*-Shrub community was found in areas transitional from wetlands to forest, or in gullies or depressions that accumulate moisture but were not necessarily wetlands. The species composition of the wetland communities in the study area at MWRS are floristically similar to those described by other researchers (Moss, 1955; Moss and Turner 1961; Jeglum 1972; Bishoff 1981; Bichlmaier 1985; Hardy and

Associates, 1986).

3.4.5 *L. ochroleucus* intensive study sites

Of the community types identified in this study, *L. ochroleucus* was a dominant component only in the forest community types. It had more than twice the per cent ground cover in the *Populus tremuloides*-dominated community than in the *Populus balsamifera*-dominated community type (Table 3.1, 3.2). *L. ochroleucus* was present in all forest sites sampled. Moss (1932) found a similar trend where *L. ochroleucus* had a higher frequency of occurrence in aspen stands (94%) than balsam stands (84%). Bishoff (1981) considered *L. ochroleucus* a distinctive species of the poplar forest community type at EINP with a 100% frequency of occurrence and mean cover of 9%. Bishoff's cover values for *L. ochroleucus* were considerably higher than those reported in this study, however the frequency of occurrence values were identical. Since *L. ochroleucus* is a prefered forage species sensitive to overuse on rangelands (Weatherill and Keith, 1969; Watson et al, 1980; Adams et al, 1986; Smoliak et al, 1988), this discrepancy in cover values may be due to the greater utilization of *L. ochroleucus* at MWRS compared to Elk Island National Park, where Bishoff conducted his study. Weatherill and Keith (1969) found *L. ochroleucus* had a 80% frequency of occurrence in the Aspen Parkland in Saskatchewan. In the data presented by Lynch (1955) for Aspen Groveland in Montana, the frequency of occurrence of *L. ochroleucus* in forested communities ranged from 1-50%. These lower values of frequency of occurrence reported by Lynch (1955) may be due to the southern location of his study plots. This may indicate the greater importance of *L. ochroleucus* in northern *Populus*-dominated forests. *L. ochroleucus* had a 3% frequency of occurrence in the grass and shrublands in the Aspen Parkland of east central Alberta (Anderson and Bailey, 1980). *L. ochroleucus* is an important species of Western Canada with its highest per cent frequency of occurrence and per cent cover occurring in the *Populus*-dominated community types. These areas dominated by *Populus* species occur in regions described by Rowe (1972) as "Aspen Parkland", "Oak Aspen Parkland", "Boreal Mixedwood', and "Lower Foothills" which together occupy over 30% of the area of the prairie provinces.

The differences in aspect, slope and site position among the *L. ochroleucus* height growth monitoring sites do not appear to have caused site differences in vegetation composition or soil development. One consideration in site selection was that they had to have an abundance of *L. ochroleucus* plants. This may, in part, account for site similarities because the ecological and environmental conditions would have to be similar enough to support an abundance of *L. ochroleucus*. Due to the similarity of *L. ochroleucus* growth monitoring sites with respect to plant species and their cover values, and soil characteristics, it is doubtful that these factors would cause differences in the growth of *L. ochroleucus* at the different sites. Thus, the influence of plant species composition and abundance, and soil characteristics among the growth monitoring sites on the production of *L. ochroleucus* was not evaluated. In addition, the *L. ochroleucus* growth monitoring sites are grouped in further analysis unless otherwise stated.

3.5 Conclusions

Within the study area at MWRS (Figure 3.1) six plant community types were identified (Tables 3.1 - 3.6). The classification (cluster and discriminant analysis) and ordination (principal components ordination) techniques used to classify the vegetation sampling sites into plant community types provided similar results (Figure 3.2). These community types are similar in floristic composition to community types identified by other researchers for the Aspen Parkland of western Canada (Moss, 1932; Lynch, 1955; Bird, 1961), especially those studies conducted on the Cooking Lake moraine (Sheffler 1976, Bishoff 1981; Bichlmaier, 1985; Hardy and Associates, 1986; Blyth and Hudson, 1987).

L. ochroleucus is an important species of the aspen and balsam poplar forests of western Canada. It had a frequency of occurrence of 100% in the *P. tremuloides* and *P. balsamifera*-dominated community types. Moss (1932), Bishoff (1981) and Weatherill and Keith (1969) have reported similar values for frequency of occurrence in these community types. *L. ochroleucus* had a higher per cent cover in the *P. tremuloides*-dominated community type than in the *P. balsamifera*-dominated community type. This trend conforms to results reported by Moss (1932) for the Parkland of central Alberta.

The three *L. ochroleucus* growth monitoring sites had similar soil and vegetation characteristics. The three sites had Orthic Grey Luvisol soils and were all classified into the *Populus tremuloides*-dominated community type based on cluster and discriminant analysis. In addition, the three *L. ochroleucus* growth monitoring sites were grouped together within the *Populus tremuloides*-dominated community type (Figure 3.2). Due to the similarity of *L. ochroleucus* growth monitoring sites with respect to plant species, their cover values, and soil characteristics it is doubtful that differences in plant species composition and soil characteristics among the sites would cause differences in the growth of *L. ochroleucus* at the different sites.

3.6 REFERENCES

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4.0 Growth Characteristics of *Lathyrus ochroleucus*

4.1 Introduction

The increase in size or weight of a plant through the growing season can be described with a simple mathematical function, and graphed as a straight line or a simple S-shaped curve (Salisbury and Ross, 1985). These relationships can be represented mathematically by either a polynomial or by one of a family of logistic relationships (Morgan, 1984). The growth functions such as the monomolecular and autocatalytic formulas, the Gompertz equation, and the parabolic or double log curve, enable the rate of growth to be described in terms of biologically meaningful parameters. These growth functions have all been shown to fit experimental data, but it has never been possible to show that any one of them fits the facts so exactly that the others can be excluded (Williams, 1964). In contrast, polynomial equations can be fit precisely and evaluated statistically (Rimmington and Charles-Edwards, 1987).

The typical S-shaped (sigmoid) growth curve illustrates three phases of herbaceous plant phytomass accumulation: logarithmic increase, linear increase and growth senescence (Figure 4.1). During the logarithmic growth phase, herbaceous plant size increases exponentially with time, while increase in size continues at a constant, usually maximum rate during the linear growth phase. In the senescent phase, growth rate decreases as the herbaceous plant reaches maturity and begins to senesce or allocate resources to reproduction or root storage.

L. ochroleucus, being a herbaceous perennial, allocates energy reserves, stored from the previous season, into vegetative growth early in the growing season. Underground storage organs such as rhizomes and roots may contain as much as 60% carbohydrate at the end of the growing season (Mooney, 1972). This carbohydrate accumulation provides reserves for new vegetative growth in the early spring resulting in a significant depletion of these reserves (Trlica, 1977). This allows the plants to

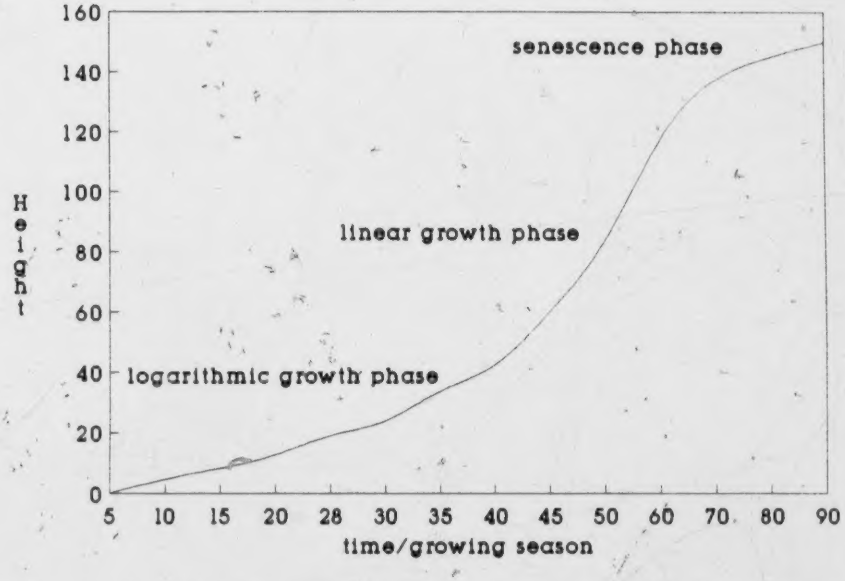


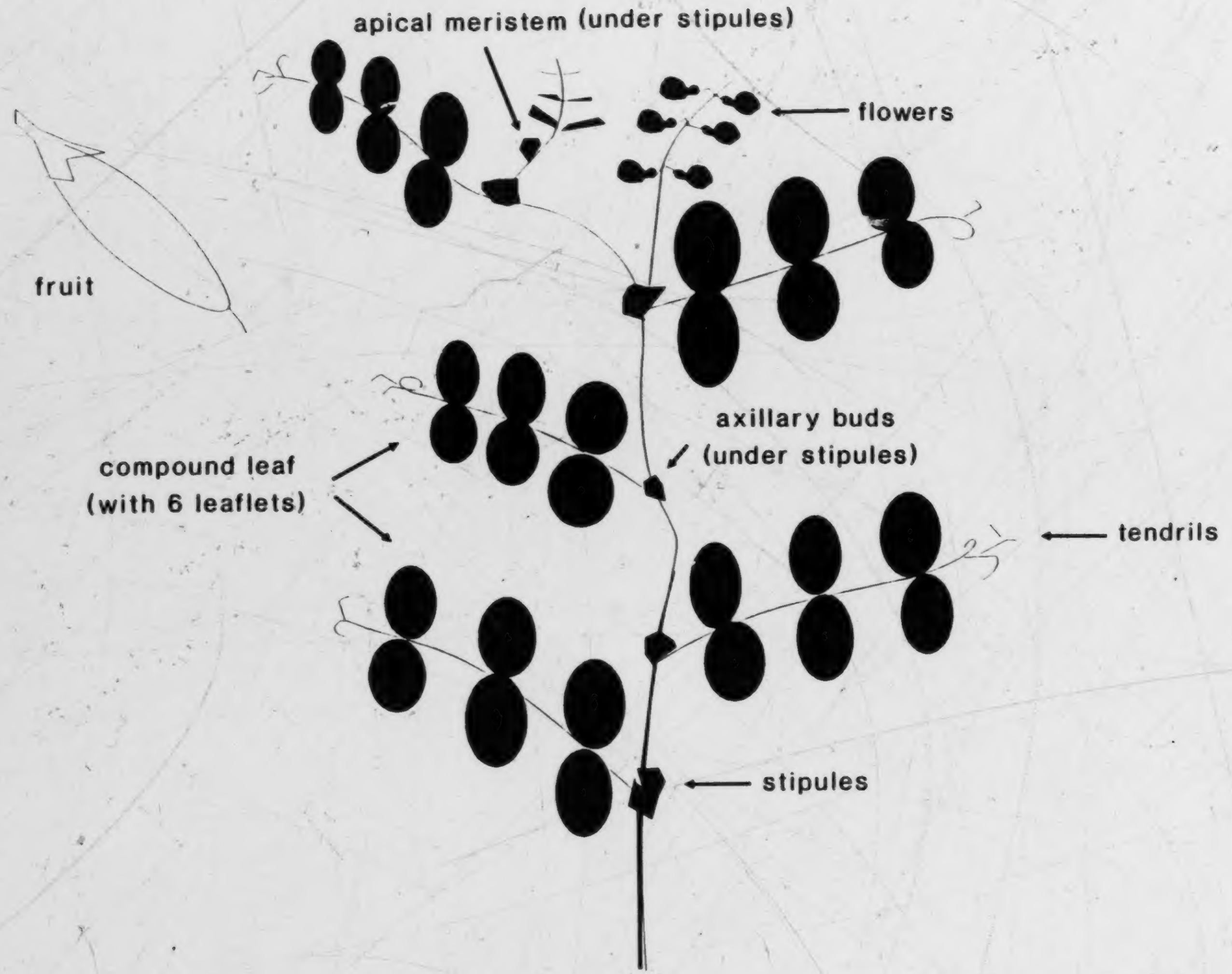
Figure 4.1 Idealized sigmoidal growth curve typical of herbaceous plants (After Salisbury and Ross, 1985).

produce their photosynthetic tissue and trap as much radiation as they can in the spring when the solar angle is high and the deciduous overstory has not yet fully developed. These new shoot systems produce assimilates that are used by the plant for further vegetative growth or are stored and later utilized when net photosynthesis can not meet the plant's demands (Trlica, 1977; Rechcigl, 1982). Once the accumulated food supply is adequate, the plant is ready to flower and reproductive structures take precedence over the storage process (Daubenmire, 1974; Trlica, 1977; Rechcigl, 1982; Nobel, 1983). Near the end of the growing season the accumulated assimilates move preferentially to the subterranean parts of the plants where they are stored until the following season (Mooney, 1972; Larcher, 1983; Nobel, 1983).

The growth of *L. ochroleucus* is initiated from the apical meristem (Figure 4.2) The apical meristem at the very tip of the stem produces on its flanks, leaf primordia at regular intervals and in a regular pattern. Along with the formation of leaf primordia, secondary meristems form in the angles between leaf primordia and the stem. These develop into axillary buds that remain dormant until well after the adjacent leaf and internode are mature. However, they can develop into lateral branches or flowers. Growth occurs by the division, differentiation, and subsequent enlargment of the cells of the meristematic tissue.

The size of a plant can be related to the amount of solar energy it receives (Beadle et al., 1985; Bunce, 1989). Generally the more leaf area the greater the potential production (Blackman, 1919; Watson, 1952; Baker et al., 1977). Plants gain weight in proportion to their existing weight and thus have an exponential weight increase during periods of unlimited growth (Blackman, 1919; Etherington, 1975). This is generally true as long as the upper leaves of a plant do not shade the lower leaves and reduce their photosynthesis to the extent that they can not support their respiratory demand. Within closed-canopied herbaceous

Figure 4.2 *L. ochroleucus* morphology, the apical meristem is the point from which stem elongation is initiated. Plant height was measured from the ground to the apical meristem.


apical meristem (under stipules)
flowers
fruit
axillary buds
(under stipules)
compound leaf
(with 6 leaflets)
tendrils
stipules

vegetation, small differences in plant height are associated with large changes in the intensity, direction, and quality of radiation they receive (Grime, 1979). Therefore, a plant that is slightly taller may receive considerably more radiation due to its superior position above competitors in the herbaceous canopy layer.

Flower and fruit development depends on the transport of reserves from roots and leaves to the maturing fruit (Shea and Watson, 1989). The amount of energy a plant has determines if it will flower provided temperature, day length, and vernalization requirements have been met (Wang 1967; Raper et al., 1988). Carbohydrate balance is dependent on assimilation (and respiration) which generally increases as radiation interception increases (Beadle et al., 1985). Therefore, within a species, larger plants which intercept more radiation and thus have the potential to produce and use larger quantities of carbohydrates should, in general, produce more fruit and have higher growth rates than shorter plants.

4.1.1 Objectives

This part of the research had three objectives:

(1) To develop a growth curve model that illustrates the phenophases and early-season growth of *L. ochroleucus*;

(2) To determine if plants that produced flowers had growth rates different from those that did not flower;

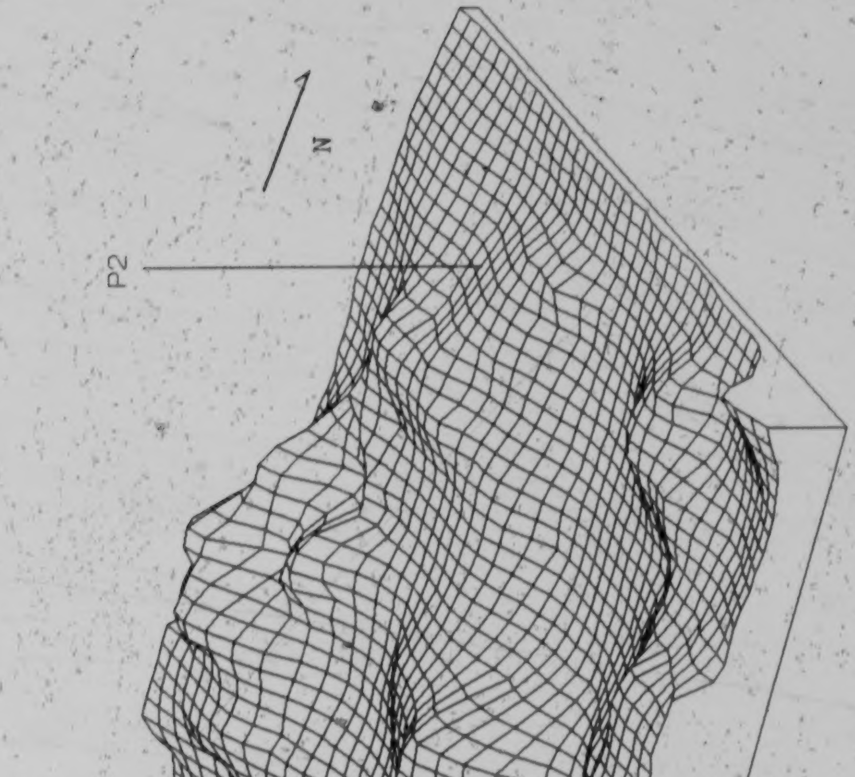
(3) To determine if the height of *L. ochroleucus* plants influences their growth rates.

4.2 Methods

Three sites were selected to study *L. ochroleucus* growth because of the abundance of *L. ochroleucus* and their proximity to previously installed microclimate stations (Figure 4.3). At each site, 90 to 130 plants were located and marked by placing a T-stake in the ground by the plant. Lines were etched on the T-stakes to act as a benchmark for measuring plant height changes. The T-stakes were pushed into the ground so the etching was at the ground level. The height of each plant was measured from May through July at approximately weekly intervals. Height of the plant was the distance from the mark on the T-stake to the highest tip of the plant when stretched, and was determined to the nearest millimetre. If axillary buds developed into branches, the length of this shoot from the main stem to the shoot tip was measured. The shoot length was then added to that of the main stem to obtain total (cumulative) plant height (length).

During each sampling interval, there were plants that did not grow or that exhibited no measurable growth. This caused the growth rate data to be positively skewed with a relatively large number of plants having a growth rate of 0. To alleviate this problem and permit the use of parametric statistics, the percentage of plants exhibiting measurable growth and their growth rates (cm d^{-1}) were analyzed separately. The proportion of plants exhibiting measurable growth for each sampling interval was obtained by counting the frequency of individuals that had an average daily growth rate of greater than 0.095 cm d^{-1}. The value of 0.095 cm d^{-1} was an arbitrarily determined cut off point.

Figure 4.3 Digital elevation model of *L. ochroleucus* study sites at MWRS. The three sites where *L. ochroleucus* was studied are labelled P1, P2, and P3. Vertical exaggeration is ten times. The spacing of horizontal lines is ten metres.


N
P2
P3
P1
765
770
775
m asl

Growth rate (cm d^{-1}) was calculated by subtracting each plant's height from its previously measured height and dividing by the number of days between the two sampling times:

$$\text{ht@T2} - \text{ht@T1} / \text{JD@T2} - \text{JD@T1} = \text{GR} \tag{1}$$

Where:

ht@T1 = Plant height at time T1 (cm)
ht@T2 = Plant height at time T2 (cm)
JD@T1 = Julian day at time T1
JD@T2 = Julian day at time T2
GR = Growth rate (cm/day)

Growth rate is a ratio scale measurement and captures more information than any other scale of measurement (Norcliffe, 1982), thus, where possible, it was used in the analyses.

Regression analysis was used to fit a growth curve to changes in plant height over the growing season because of its great advantage over traditional growth functions due to its ease of calculation and statistical evaluation. First, second, and third degree curvilinear regression models were used to produce plant height growth models for each of the three sites separately, and then with the data grouped.

The relationship between the growth rate of plants that flowered and those that did not was investigated using one-way analysis of variance (ANOVA) for each sampling interval. For each sampling interval one-way ANOVA tests were performed to determine the significance of growth rate variability between the plants that flowered and those that did not.

The effect of plant height on the proportion of plants growing and their growth rates was investigated using correlation analysis. A separate analysis was conducted on the relationship between plant height and growth rate and similarly between plant height and the proportion of plants growing. These analyses were conducted for both the linear and the reproductive/storage phases of growth. In addition, correlation coefficients were used to evaluate the relationship between height and growth rate for each sampling interval.

4.3 Results

4.3.1 *Lathyrus ochroleucus* Growth Curve

When the height of *L. ochroleucus* was plotted against date the resulting graph approximated a sigmoid curve without the logarithmic phase (parabola). First, second, and third degree curvilinear regression models were used to produce plant height growth models (Table 4.1). When the regression models were applied to the sites separately, site P3 was the only one where the models could significantly explain the growth characteristics of *L. ochroleucus* ($P < 0.05$). The variance explained by these models, however, was small (Table 4.1). When the sites were grouped and the same curvilinear models applied, all curves accounted for some of the variation in the growth of *L. ochroleucus* at a significant level. The curve produced with the second degree polynomial equation best represented the seasonal growth characteristics of *L. ochroleucus* (Table 4.1 and Figure 4.4). This model, however, explained only 38% of the variation in the growth of *L. ochroleucus* (Table 4.1).

Table 4.1. Results obtained from fitting growth curves to *L. ochroleucus* height data with the use of regression models, MWRS, 1989.

Site	Model	r^2	prob>F
all sites	1st. degree	0.0079	0.0147
	2nd. degree	0.3760	0.0001
	3rd. degree	0.0086	0.0389
P1	1st. degree	0.0102	0.1069
	2nd. degree	0.0167	0.1193
	3rd. degree	0.0167	0.1193
P2	1st. degree	0.0049	0.1069
	2nd. degree	0.0049	0.5135
	3rd. degree	0.0050	0.7190
P3	1st. degree	0.0332	0.0034
	2nd. degree	0.0049	0.0117
	3rd. degree	0.0389	0.0117

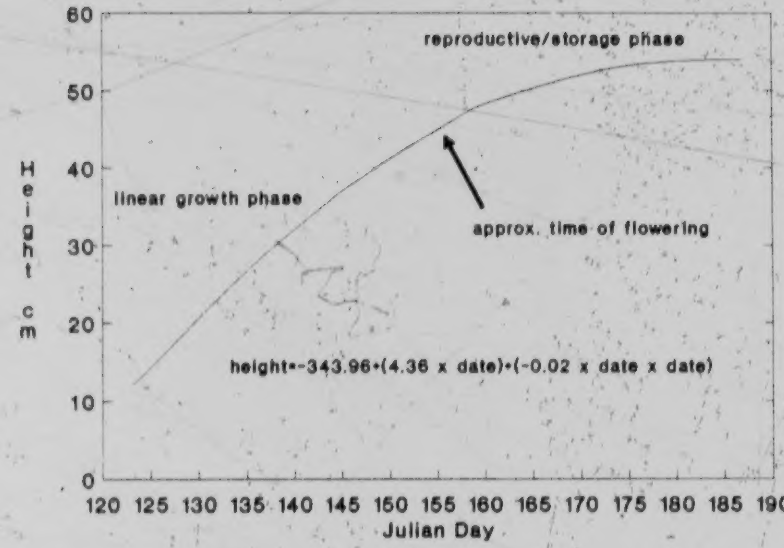


Figure 4.4 *L. ochroleucus* height growth curve fit with 2nd degree polynomial equation, MWRS, 1989. Data are combined for all three sites. Supplemental data for this model is in Appendix II.

The following analyses are conducted with all *L. ochroleucus* height growth monitoring sites grouped unless otherwise stated.

4.3.2 The Effect of Plant Height on the Proportion of Plants Growing and their Growth Rates.

A separate analysis was conducted on the relationship between plant height and growth rate for the two growth phases. Plant height and the per cent of plants growing had a negative correlation during both growth phases. However, during the reproductive phase the relationship was not significant ($P=0.05$). Plant height accounted for 11% ($P < 0.0001$) of the variability in the per cent of plants growing during the linear growth phase.

Plant height had a negative correlation with growth rate in both the linear and reproductive/storage phases of growth ($P < 0.02$). The variation in growth rate accounted for by height was similar, though small, for both growth phases: $r^2 = 0.022$ for the linear phase and 0.028 for the reproductive phase. When the relationship between plant height and growth was analyzed separately for each sampling interval, the correlations varied with no clear trends apparent (Figure 4.5). Plant height had a positive correlation with growth rate during the first two sampling intervals and a negative correlation during the 3rd and 4th intervals after which time the relationship again became positive during the 5th and 6th sampling intervals (Figure 4.5). During the last three sampling intervals, the correlation between *L. ochroleucus* height and its growth was negative although not statistically significant. When the correlation coefficients between height and the per cent of plants growing were determined for each sampling interval, no significant relationships were found.

The growth rates of the plants that flowered were higher than those of the plants that did not flower, except during the 7th, 8th and 9th sampling intervals (Figure 4.6). Of the 24% of the plants that

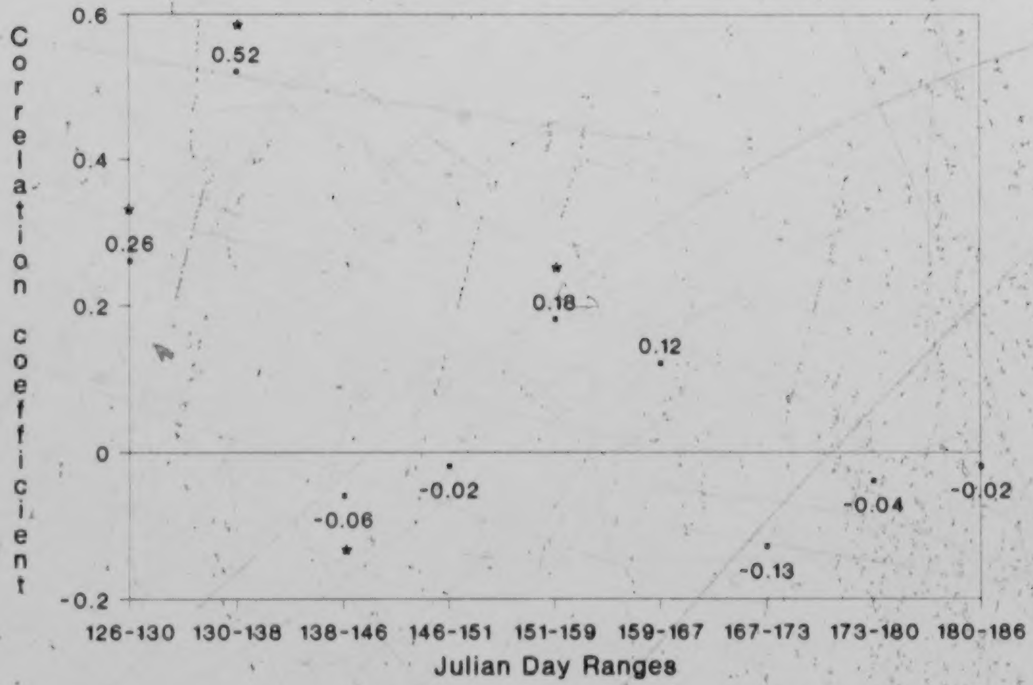


Figure 4.5. Correlation between *L. ochroleucus* height and growth rate, MWRS, 1989. Height at the beginning of the sampling intervals was analyzed with the height growth rate during the sampling interval to determine significant relationships. Significant ($P < 0.05$) correlations indicated with *.

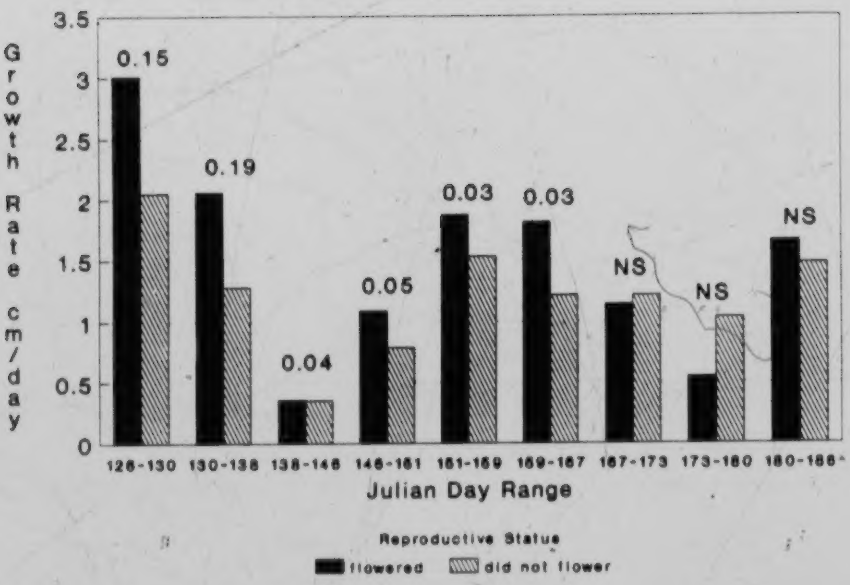


Figure 4.6 Growth rate comparison between *L. ochroleucus* plants that flowered and those that did not, MWRS, 1989. The numbers above the bars represent the per cent variability in growth rate accounted for by flowering (determined by ANOVA). NS=not significantly different ($P < 0.05$).

flowered, 90% produced flowers between 6 and 12 June.

4.4 Discussion

The growth curve that best fits the height data collected for *L. ochroleucus* had two distinct growth phases (Figure 4.4). During the first phase (linear phase) which occurred early in the spring, the plants exhibited their maximum growth rate. This linear phase continued for approximately 5 weeks at which time growth slowed and the second distinctive phase (reproductive/storage phase) commenced. At the beginning of the linear growth phase, which occurred early in the growing season, plant growth is more dependent on stored reserves than upon the amount of photosynthesizing tissue. Early spring rapid expansion of the leaf canopy characteristic of many perennial herbs is the result of the mobilization of large reserves of energy and structural materials accumulated in underground storage organs during the later stages of the previous season (Grime, 1979). This allows the plants to produce their photosynthetic tissue and trap as much radiation as they can in the spring when the solar angle is high and the deciduous overstory has not fully developed. This dependence on reserve carbohydrates from the previous growing season for early spring growth is common in many perennial plants (McCarty, 1938; McIlvanie, 1942; Mooney and Billings, 1960; Kimura, 1969; Mooney, 1972), including legumes (Graber et al., 1927; Grandfield, 1935; Smith, 1962; Nelson and Smith, 1968; Smith and Silva, 1969).

It is unknown how the stored reserves from the previous season are partitioned between ramets of *L. ochroleucus* that are interconnected through an intricate root/rhyzome network. This colonial growth pattern of *L. ochroleucus* means that a group of ramets (collectively called genets) are genetically identical and to some degree interdependent on resources (Kays and Harper, 1974). Harvey (1979) in studying *Trifolium repens* concluded that there was a common pool of carbohydrate resources from which all ramets could draw (From: White, 1984). While Newell (1982) showed that the degree of physiological integration varied among stoloniferous species of *Viola* (From: White, 1984). The allocation of energy reserves and assimilates within the plant or between shoots of colonal plants would improve our understanding of the processes influencing *L. ochroleucus* growth and development. This, however was outside the scope of this study.

During the different phases of growth the physiological functions of the plants change to meet their specific needs (Nobel, 1983). Different hormones become active and their concentrations change as a plant moves from vegetative to reproductive production (Salisbury and Ross, 1985). This was approximately at the same time the slope on the height growth-curve began to level out and the reproductive phase began (Figure 4.4). Regardless of whether the plants flowered, the average rate of height growth decreased. This may indicate that even if the plants did not flower they were storing a larger portion of their assimilated energy at this time.

The plants that flowered had significantly higher growth rates before flowering than the plants that did not (Figure 4.6). With higher growth rates, the plants that did flower were larger and had more leaf area to intercept photosynthetically active radiation (PAR). Since assimilation is proportional to PAR interception (Beadle et al., 1985), which is in turn closely related to leaf area, the plants that flowered, being larger, would produce more carbohydrates than smaller plants. This greater carbohydrate production in the larger *L. ochroleucus* plants could provide the necessary reserves needed for sexual reproduction. The amount of energy reserves a plant has is one of the factors which determine if it will flower (Wang, 1967; Raper et al., 1988). Generally, the plants with the lower growth rates did not have the advantages associated with larger size and did not accumulate the reserves necessary for sexual reproduction. Carbohydrate supply to the meristems must be greater to support floral development than for the continuation of vegetative growth (Sachs and Hackett, 1983). A portion of the plants that did not flower may have been seedlings and thus would not have the previous season's energy reserves to draw upon for early spring vegetative growth.

Following flowering, the plants that produced reproductive structures did not have height growth rates that were significantly greater than the plants that were infertile. This may be due to the allocation of resources to developing seeds. Successful fruit development depends on the transport of reserves from the roots and leaves to the maturing fruits (Mooney and Billings, 1960; Jameson, 1963; Trlica, 1977; Moser, 1977; Rechcigl, 1982; Noble, 1983; Raper et al., 1988; Shea and Watson, 1989). Resource/energy sinks appear to compete with one another for photosynthate (Moser, 1977; Raper et al., 1988) so the strong "drawing power" of the maturing seeds of *L. ochroleucus* would reduce the resources available for vegetative growth.

The growth rate of the plants that did flower was significantly higher than that of the sterile plants. Flowering, however, only accounted for a small portion of the variability in growth rate. Although the plants that flowered were generally larger than those that did not, the relationship between plant height and growth requires discussion.

During the first and second sampling intervals height of *L. ochroleucus* was positively correlated with its growth rate. The larger plants had greater leaf area and thus intercepted more PAR which increased photosynthesis resulting in increased dry matter production. Several researchers have reported that early in the spring before canopy closure many crops exhibit a linear relationship between the interception of solar radiation which increases with leaf area index and the production of dry matter (Watson, 1952, 1958; Donald and Black, 1958; Jameson, 1963; Ashley et al., 1965; Baker and Meyer, 1966; Shibles and Weber, 1966; Hesketh and Baker, 1967; Bjorkman, 1981). After canopy closure the relationship between interception and leaf area is no longer linear (Beadle, 1985), and shading by overstory as well as by neighbouring understory species will affect growth.

The height of ramets of *L. ochroleucus* will influence their degree of shading by other understory species. The increased shading of shorter plants will influence their growth rates, since a plant that is slightly taller may receive considerably more radiation due to its superior position (above competitors) in the understory (Grime, 1979; Etherington, 1984).

Shade under deciduous woodlands involves a decrease in the amount of PAR, coupled with a reduction in the ratio of red to far-red radiation (R/FR ratio) (Coombe, 1957; Fedder and Tanner, 1966; Tasker and Smith, 1977). Although a reduction in PAR reduces growth (Blackman, 1956, 1968), the relationship is not proportional because of compensatory changes in plant development such as specific leaf area (Mitchell and Woodward, 1988) and at the biochemical level, photosynthesis (Bjorkman, 1981). Increased compensatory developmental changes in shorter *L. ochroleucus* plants relative to the larger plants would reduce the growth rate differences caused by the advantages of size, whereby the larger plants having a superior position within the herbaceous canopy receive more PAR. The R/FR ratio determins the ratio between the two photoconvertible forms of phytochrome (Larcher, 1983). The ratio between the two states of phytochrome regulates gene activity and thus the various eventual reactions that govern plant response (Larcher, 1983). Plants may respond to low R/FR ratios with an increase in stem or petiole length (Holmes and Smith, 1977; Morgan and Smith, 1981). This response, however, is muted in species characteristic of shady habitats (Fitter and Ashmore, 1974; Morgan and Smith, 1979; Smith, 1982). *L. ochroleucus*, being a species common to moist woods as well as clearings (Moss, 1983; Coupe et al., 1982), may respond to decreasing

R/FR ratios (caused by increased shading) by an enhanced rate of stem elongation. If leaf area, the rate of photosynthesis, and stem elongation increase more in the shorter than the larger *L. ochroleucus* plants in response to changes in shading resulting from the closure of the herbaceous canopy, then this may help explain why larger plants did not have higher growth rates than smaller plants between Julian day 138 and 151 (Figure 4.5). The understory of the aspen-dominated forest at MWRS had sufficient time for vegetative production by this time in the season so competition with *L. ochroleucus* plants for the light resource could have been significant.

Carbohydrate balance of *L. ochroleucus* plants may also help explain the negative correlation between height and growth during the 3rd and 4th sampling intervals (Julian day 138 to 151). The quantity of carbohydrate reserves in forage plants is inversely related to herbage growth (Smith and Silva, 1969; Trlica, 1977). Presumably the stored energy reserves from the previous season in the smaller *L. ochroleucus* plants became depleted before those in the larger plants during their utilization in early spring vegetative production. The physiological functions of the plants may have had to adjust to reduced resource levels once the previous year's storage reserves were depleted. Thus, growth rate would be positively correlated with height in the early season when the smaller plants were adjusting to reduced resource levels and negatively correlated later when the larger plants were adjusting. As well, with larger plants being predisposed to flowering, they may have been storing a larger portion of their assimilates during the 3rd and 4th sampling intervals in preparation for sexual reproduction. Generally, the smaller plants did not flower and thus would not require energy reserves for reproduction and could utilize assimilates for vegetative growth.

After the negative correlation between height and growth rate during the 3rd and 4th sampling intervals, the height of *L. ochroleucus* had a positive correlation with growth rate until approximately one week after flowering. Subsequent to flowering these plants, which tended to be larger, were allocating energy to seed development rather than vegetative growth (Jameson, 1963; Trlica, 1977; Moser, 1977; Rechcigl, 1982; Nobel, 1983; Raper et al., 1988; Shea and Watson, 1989). Therefore, the increased amount of PAR received by larger plants would not be proportional to growth rate because of reproductive resource allocation. This may explain the significant, but weak, negative correlation between plant height and growth rate during the reproductive growth phase when the sampling intervals were grouped.

4.5 Conclusions

The height growth of *L. ochroleucus* can be represented with the use of a second degree polynomial equation. This growth curve model had two distinct growth components: the linear-vegetative and the reproductive/storage phases. These phases are reflective of the changing physiological functions of the plant and the partitioning of resources to meet these specific needs. The linear phase was dominated by vegetative growth while the reproductive/storage phase was dominated by reproductive growth and assimilate storage.

The strength of influence that plant height has on the proportion of plants growing and their growth rates is dependent on the growth phase governing the plant. Generally plant height is not a dominant factor governing the proportion of *L. ochroleucus* plants growing and their growth rates except early in the growing season when growth rate is most strongly influenced by plant height. This positive correlation can be explained by the phenomenon whereby larger quantities of reserve energy stored from the previous growing season produce larger plants with greater leaf areas. This occurs early in the spring when this energy stored from the previous season is utilized for rapid vegetative growth. With assimilation being proportional to PAR interception, which, in turn, is closely related to leaf area, the larger plants would accumulate more carbohydrates than the smaller plants and thus continue to exhibit higher growth rates. Since the plants that flowered tended to be larger than the plants that did not flower, it follows that the flowering of *L. ochroleucus* is largely dependent on the quantity of energy reserves accumulated during the previous growing season. The positive relationship between height and growth rate changes after the early season vegetative flush. This may be influenced by:

> (1) The disproportionate increase in shading of smaller compared to larger *L. ochroleucus* plants as understory canopy closure increases;
>
> (2) Physiological adjustments to the reduced resource levels once the previous seasons stored reserves have been depleted which occurs later in larger plants;
>
> (3) The greater allocation of carbohydrates to storage in the larger plants in preparation for reproductive development.

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5.0 The Influence of Environmental Factors on the Growth and Production of *Lathyrus ochroleucus*

5.1 Introduction

A knowledge of the response of the individual plant species to the environment in which they live is an essential prerequisite to the proper management of our rangeland resources (Tueller, 1977; Sosebee, 1977). Little quantitative information is available on the relationship between the growth of *Lathyrus ochroleucus* and environmental factors. *L. ochroleucus* is an important forage species for wapiti and deer as well as cattle. It is preferentially selected (Blood, 1966; Weatherill and Keith, 1969; Hunt, 1979; Watson et al., 1980) and utilized much in excess of its availability (relative to other forbs) (Weatherill and Keith, 1969). This study focuses on the influence of environmental factors on *L. ochroleucus* growth during the spring when it is most highly utilized (Blood, 1966; Weatherill and Keith, 1969). High quality forage is essential to animals in spring due to their low nutritional status after winter energy deficits (weight loss) (Murie, 1951; Quimby and Johnson, 1951). A better understanding of the affects that environmental factors have on the growth and production of *L. ochroleucus* will assist in formulating management strategies to maximize its utilization as forage while at the same time maintaining its production.

Phenology is the study of plant growth and development and the cause of their timing with regard to biotic and abiotic influences. Analysis of plant phenology, quantitatively and qualitatively, can help determine the degree to which environmental factors, both individually and collectively, influence the vital growth and development processes of a plant (Newman and Beard, 1962).

Many researchers have focused their attention on the influence of temperature in plant growth and development studies (Hopkins, 1938; Went, 1953; Nuttonson, 1953; Lindsey and Newman, 1956; Brown, 1960; Wang, 1960; Jackson, 1966; Abrami, 1972). Went (1953) stated " Almost half of all published papers in plant physiology ... contain references to temperature ...". Temperature is commonly recognized as the key factor in plant productivity (Rechcigl, 1982; Smith, 1975).

Plant growth is regulated by the many individual chemical reactions controlling total plant metabolism (Treshow, 1970). The effects of temperature on the plant are largely mediated by their effects on chemical reactions (Went 1953). The ratio of the rate of a chemical reaction at a given temperature to its rate at a temperature 10° C lower or higher is called the temperature coefficient (Q_{10}). The Q_{10} of a particular process can be indicative of the minimum energy required for that process (Nobel, 1983). Cell growth, especially cell elongation, has a high Q_{10}, which indicates that this is a chemically rather then physically controlled phenomenon (Went, 1953). Growth is largely influenced by the two fundamental metabolic processes of photosynthesis and respiration (Treshow, 1970). Increases in temperature usually increase photosynthetic rates until enzyme denaturation and photosystem destruction begin (Salisbury and Ross, 1985). However respiratory CO_2 loss, especially through photorespiration, increases relative to photosynthesis as temperature increases. Thus, at lower temperatures, the ratio of photosynthesis to respiration is over 10, at higher temperatures respiration is increased relatively more and thus low P/R ratios are found (Went, 1953). In general, optimal temperatures for photosynthesis are similar to the daytime temperatures at which the plants normally grow, except that in cold environments the optima are usually higher than air temperatures (Salisbury and Ross 1985).

Many researchers have stressed the importance of moisture in plant growth and development studies (Baier, 1965; Smith, 1975). After an extensive review of the relevant literature, Baier (1965) concluded that those studies which include moisture are the most promising as a basis for evaluation of plant production potential and crop forecasting.

Extensive evidence exists which supports the concept of gradual reduction of growth by decreasing potential (Richards and Wadleigh, 1952; Stanhill, 1957; Etherington, 1975). Photosynthesis is reduced even by relatively small water deficits and certainly by water potentials higher than -1.5 MPa (Etherington, 1975). A plant withdraws water from the soil only as long as the water potential of it's fine roots is more negative than the soil solution (Larcher, 1983).

The different phases of growth are influenced by various combinations of environmental factors because each stage differs in its physiological function. With approximately 80% of plant height growth occurring in the spring during the linear phase of *L. ochroleucus* development, it becomes the most important phase in forage production. As well, several researchers have reported that *L. ochroleucus* is most highly utilized by wapiti and cattle during the spring (Blood, 1966; Weatherill and Keith, 1969). It is therefore important to develop a mechanism for predicting or approximating the developmental stages and production of *L. ochroleucus* from environmental variables during this time. It has been found that each plant species requires a constant accumulated temperature or degree days above a specific threshold temperature to reach a certain stage of development (Pearson, 1924; Nuttonson, 1953; Lindsey and Newman, 1956; Jeffree, 1959; Newman and Beard, 1962; Jackson, 1966). Therefore, degree days (GDD) can be used to predict the time a specific developmental stage should be reached. In addition, GDD can be used to predict productivity (Bauer et al., 1984; George et al., 1988). If workable, these models could be applied to similar environments under different temperature regimes. This would assist in estimating the quantity of *L. ochroleucus* available for ungulate foraging during the spring.

5.1.1 Objectives

Within the context outlined above, the following objectives were formulated:

1. Determine an appropriate scale of analysis by comparing meso and microclimate influences on the variability of *L. ochroleucus* growth rate;

2. Determine the relationship between soil and air temperature and the growth of *L. ochroleucus*;

3. Determine the influence soil moisture variability has on the growth of *L. ochroleucus*;

4. Develop a methodology that can be used to predict the productivity of *L. ochroleucus* on an areal basis.

5.2 Methods

5.2.1 Temperature and Soil Moisture

Daily temperature data were collected through the use of automated data loggers that were centred at all three of the *L. ochroleucus* growth monitoring sites. Thermocouples for measuring air temperature were mounted in small Stevenson screens at 1.5 m above the ground. Soil thermocouples were at a depth of 20 cm from the top of the mineral soil. The variables used for both air and soil temperatures were the following:

- maximum daily temperature
- minimum daily temperature
- mean daily temperature (max+min/2)

The arithmetic mean of max., min., and mean daily air and soil temperatures were calculated for each sampling interval that growth rate was determined for. The mean daily air temperatures were summed for each day within each sampling interval to obtain the GDD for each sampling interval.

Soil moisture samples were collected around the periphery of *L. ochroleucus* monitoring sites at a depth of 20 cm each time plant measurements were recorded (approximately weekly). Three samples were taken from each site. The sample's wet weights were obtained then they were dried at 105° C for 48 hours. Water content was calculated as a percentage of weight:

$$\text{water content (wt.\%)} = \frac{\text{moist wt.} - \text{oven-dry wt.}}{\text{oven-dry wt.}} * 100 \qquad (1)$$

The mean was calculated for the three samples from each site. Each site's soil moisture was graphed against time (date) and soil moisture was estimated for each day through interpolation. The average soil moisture content was then calculated for each sampling interval.

5.2.2 Soil Description and Classification

Soil pit descriptions were performed at each of the *L. ochroleucus* growth monitoring sites. The soil descriptions follow the methodology outlined by the Expert Committee on Soil Survey (1983). Soils were classified according to the Canadian System of Soil Classification (Canadian Soil Survey Committee, 1978).

5.2.3 Plant Growth Data and Parametric Statistics

The method of collecting *L. ochroleus* height measurements, and the calculation of growth rates and percentage of plants growing was outlined in Chapter 4.

The Sharpo-Wilk statistic (n<51) or the Kolomogorov D statistic (n>51) was used to test the probability ($P < 0.15$) that the data used in the following analysis were a random sample from a normal distribution (SAS Institute Inc., 1985). If the data were not normally distributed according to the above mentioned tests, then data transformations were performed to meet the test's normality requirements. When using variables measured at an interval or ratio scale, a parametric test is more powerful than a nonparametric test for a given sample size provided the test's assumptions are met (Norcliffe, 1982). The only variable that required transformation was growth rate. The natural log of growth rate suitably shifted the distribution to allow the use of parametric statistics.

5.2.4 Scale of Analysis

The per cent of plants exhibiting height growth and height growth rate data were analyzed separately as the dependent variable in several one-way analysis of variance (ANOVA) models. The classification variables that were used were site and time. The site classes were the growth monitoring sites and the time classes were the intervals between sampling dates. Comparison of the variability in growth characteristics accounted for by time and site, help determine the relative importance of microclimatic differences between sites compared to mesoclimatic patterns that influence all the sites.

5.2.5 Growth Phases and Growing Degree Days

The duration and timing of the linear growth phase was evaluated in terms of GDD above 0^{o} C. Although this information is descriptive and not statistically based, it was used to estimate the timing of the development phases of *L. ochroleucus* in terms of heat units.

Five different base temperatures were used in determining the minimum threshold temperature above which mean daily temperatures were summed. These base temperatures were 0^{o}, 1^{o}, 2^{o}, 3^{o}, and 4^{o} C. Correlations between the different growing degree day (GDD) summations (resulting from different base temperatures) and growth rate resulted in coefficients that were not significantly different (F test, P=0.05).

This is consistent with results that other researchers have reported for several different species. They found that by changing the threshold values there was no improvement in the correlation between heat units and the target species growth characteristics (Wang, 1958; Thornthwaite, 1952). It, therefore, is reasonable to use a temperature of 0° C as the base temperature.

In the pea plant (same family as *L. ochroleucus*), there is a high negative correlation (0.8-0.9) between average daily temperature and the duration of the vegetative period (Makasheva, 1986). This is a standard pattern supported by many researchers for many species (Pearson, 1924; Nuttonson, 1953; Lindsey and Newman, 1956; Jeffree, 1959; Newman and Beard, 1962; Jackson, 1966). Although the use of heat units has been subjected to serious criticism ; it is still in widespread use to schedule planting and predict crop maturity in the canning industry and to schedule spraying programs for insects, disease and weed control as well as in the selection of suitable farming areas and the appropriate plant varieties to grow in those areas (Wang, 1960). The heat unit system has been widely adopted because of its value in satisfying practical needs, rather than for its accuracy or its theoretical soundness (Wang, 1960). In this context, the heat unit system was used as a simple method to approximate the timing and duration of the linear growth phase of *L. ochroleucus*.

5.2.6 Temperature, Soil Moisture and Growth Rate

Correlation analysis was used to evaluate significant relationships for the percentage of plants showing height growth and their height growth rate with the following variables:

soil moisture
maximum air temperature
minimum air temperature
mean air temperature
maximum soil temperature
minimum soil temperature
mean soil temperature

Although correlation analysis assists in determining the potential degree of influence temperature variables have on growth characteristics, insight is not provided as to the functions that are occurring. A crop response model for each single element, such as temperature, should be established to obtain an overall comprehensive picture of plant response to that element (Wang, 1967). Simple regression models were used to gain an understanding of the functional relationships between temperature variables and growth characteristics. Second degree curvilinear regression models were developed to represent the relationship between the air and soil temperature variables and growth characteristics. The curvilinear models, however, were used only if they explained more variation at a significant level (F test, $P=0.05$) than the simple linear regression models.

5.2.7 Relationship Between *L. ochroleucus* Height and Weight

A survey was conducted to determine *L. ochroleucus* plant density and to collect plants for the investigation of height-weight relationships. Six sites were selected due to their proximity to existing microclimate stations. At each site a 1×1m quadrat was randomly placed on the ground five times. This was done by standing in the plot centre and facing the direction of a randomly chosen compass bearing, then a random distance was chosen and the quadrat was placed that distance from the plot centre in the chosen direction. Each time the quadrat was placed the number of *L. ochroleucus* individuals was recorded. In addition, the above-ground portion of each plant was harvested. Several specimens were selected in the lab from each quadrat, to a maximum of five, in an attempt to represent the variability in age, size and stage of development. The height of these plants was measured and their oven-dry weight determined by drying at 100° C for 48 hours. A regression model was developed to predict plant weight from height data. This prediction model was used to estimate plant biomass because plants monitored in the field could not be harvested each time weekly height measurements were recorded.

5.2.8 *Lathyrus ochroleucus* Productivity

The productivity of *L. ochroleucus* during its linear growth phase was determined using average plant height, plant density, and a prediction model for estimating dry weight from height data. Average height was converted to oven dry weight with the use of a second degree polynomial equation. The production rate (PR) was expressed as the increase in dry matter per unit area per unit time. In range management terminology, production is often expressed as fresh weight. Since *Lathyrus* is 83 to 84% water (Makasheva, 1986) the fresh weight was calculated from the oven dry weight by the following formula:

$$\text{Fresh weight (g)} = \frac{\text{oven dry weight(g)} * 100}{16.5} \qquad (2)$$

Once the average weight per plant was calculated it was expressed on an areal basis by multiplying by plant density (plants m^{-2}). Plant density was determined by randomly placing a 1×1 m quadrat in plant communities that had a tree cover of greater than 40% of which no less than 50% was *Populus tremuloides*. Each of the fifty times the 1×1 m quadrat was randomly placed the frequency of *L. ochroleucus* was noted. Production rate was expressed on an areal basis in dry (g m^{-2} d^{-1}) and fresh weight (kg ha^{-1} d^{-1}).

5.3 Results and Discussion

5.3.1 Site Characteristics and Scale of Analysis

5.3.1.1 Results

When growth rate was compared amongst the three sampling sites, only 1.1% of the variability in *L. ochroleucus* growth rate was attributable to site differences (Figure 5.1). Growth rate variability among sites was analyzed separately for the different growth phases. During the linear phase, 1.2% of the variation in growth rate was due to site differences. During the reproductive/storage phase (after julian day 159) (Figure 5.1), there appeared to be more variability in growth rate among sites than during the linear phase. However, these differences were not statistically significant (*P*=0.22). The reason there was no statistical significance was because, accompanying the increased variability between sites, there was an increase in the variability within the sites. Site differences had no significant effect on the variation in the per cent of the plants exhibiting height growth when all plants were analyzed over the entire sampling season (*P*=0.098) (Figure 5.2). The variability in the proportion of plants growing among sites was greater during the linear phase (7.8%) than during the reproductive/storage phase (2.0%). Although these values were statistically significant (*P* < 0.05), they were small. Overall the differences in the variability in the proportion of plants growing and growth rate among sites was small.

When the proportion of the variability in the per cent of plants growing and growth rate accounted for by time and site in one-way ANOVA models were compared, temporal (sampling interval) variability accounted for approximately 2100% more variation in the growth characteristics than did variability among sites (Figure 5.3b). Temporal variability accounted for 39% and 1.6%, respectively, of the variation in *L. ochroleucus* growth rate during the linear phase and reproductive/storage phase, and 82% and 78%, respectively, of the variation in the per cent of plants growing during the linear phase and reproductive/storage phase (*P*=0.0001) (Figure 5.3a).

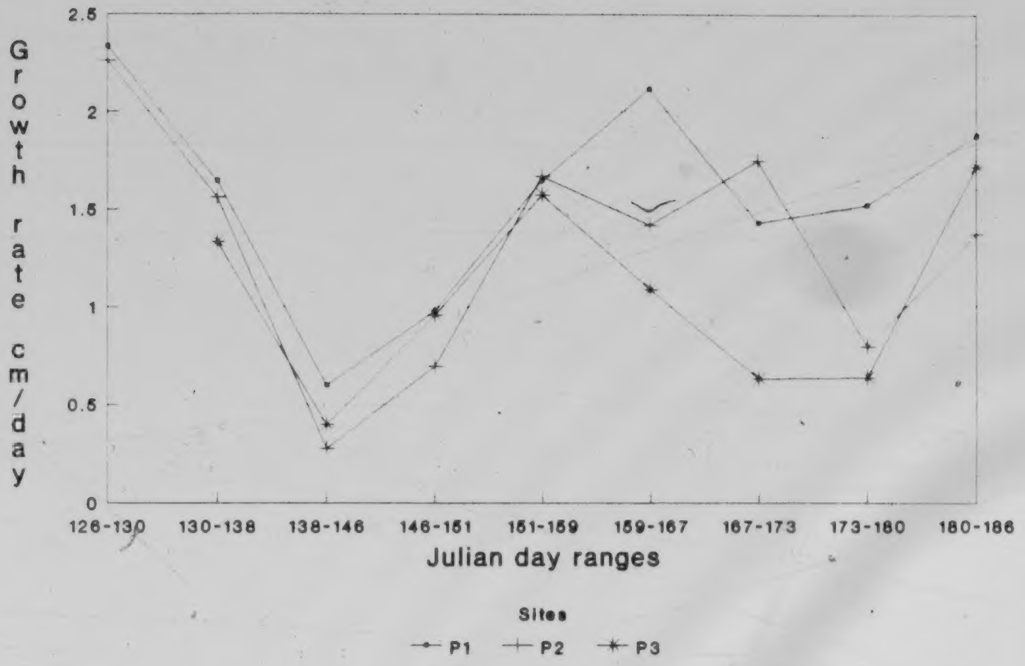


Figure 5.1 *L. ochroleucus* growth rate comparison among sites. During the linear growth phase (before julian day 159), 1.2% of the variability in *L. ochroleucus* growth rate was accounted for by sampling sites. During the reproductive/storage phase (after julian day 159), the growth rate variability among sites was not statistically significant ($P = 0.22$).

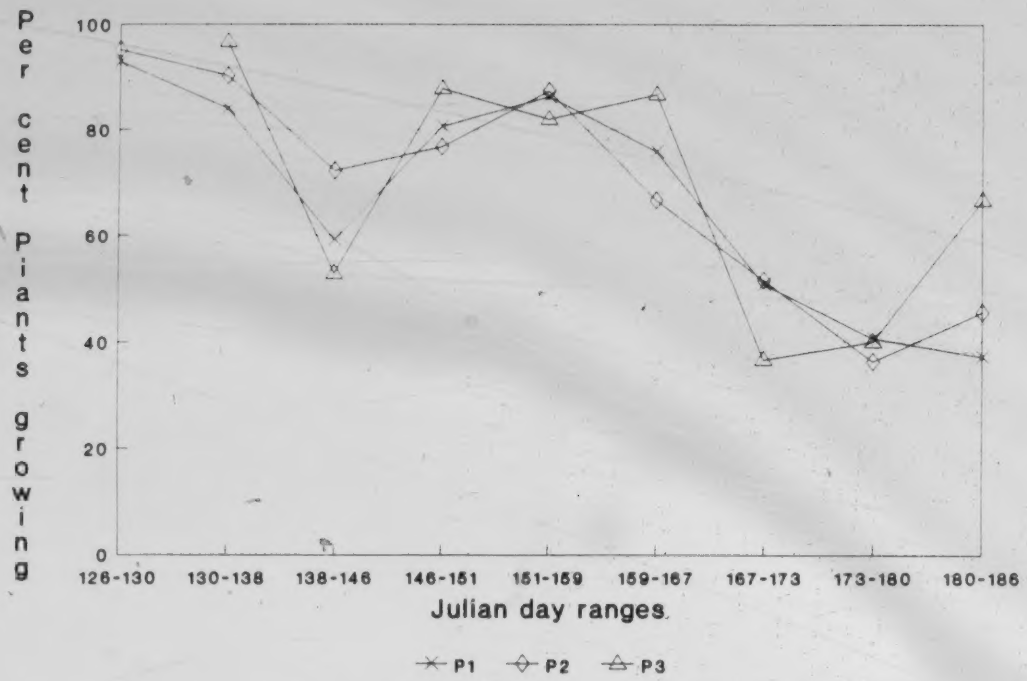
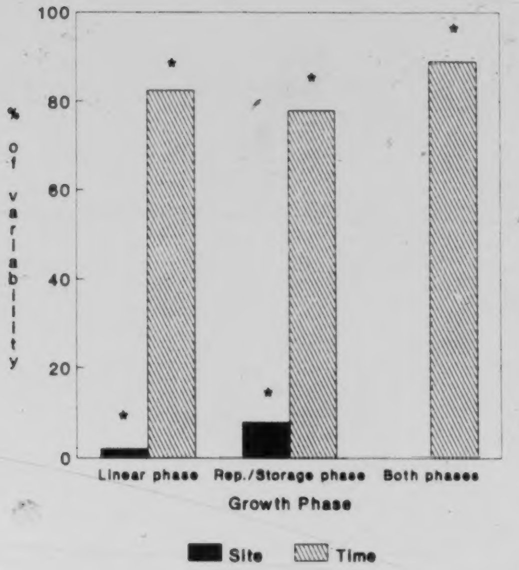
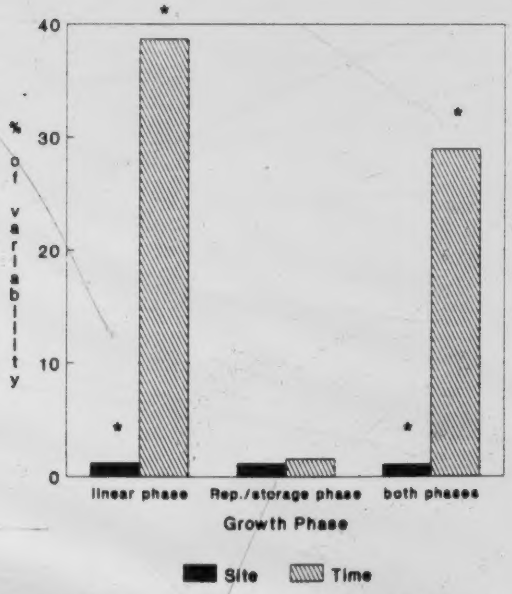


Figure 5.2 Comparison of the per cent of *L. ochroleucus* plants showing height growing among the sampling sites. The variability in the proportion of plants growing among sites during the linear growth phase (before julian day 159) (7.8%) was greater than during the reproductive/storage phase (after julian day 159) (2.0%, $P < 0.05$).

(a) Variability in Percentage of Plants Growing by Time and Site



(b) Proportion of Growth Rate Varability by Time and Site



* significantly different ($P < 0.05$)

Figure 5.3 Comparison of the variability in growth of *L. ochroleucus* accounted for by sampling time and site.

5.3.1.2 Discussion

The site differences in microclimate had a small degree of influence on growth characteristics. This is portrayed by the small amount of variability among the sites in the proportion of plants growing and their growth rates. The growth characteristics of *L. ochroleucus* at the different sites were influenced, to a large degree, by regional weather patterns. Sampling time accounted for an average of 3700% more of the variability in growth characteristics than the sampling sites did during the linear phase and an average of 575% during the reproductive/storage phase. This indicates that mesoclimatic influences of the regional weather patterns were approximately 21 times stronger in their influence on *L. ochroleucus* growth characteristics than microclimatic differences among the sample sites. This suggests that official meteorological records which reflect mesoscale climate may be usefully applied in evaluating *L. ochroleucus* growth during the early growing season. Lindsey and Newman (1956) after a statistical analysis using official temperature data to evaluate the relationship between phenology and temperature concluded:

> ... a sufficiently close parallelism exists between the official meteorological records and temperatures actually influencing the plant for such records to be ecologically useful when interpreted by a suitable method.

The temporal influence of changing weather patterns that influence the sites together at a mesoclimatic scale was the focus in further analysis.

5.3.2 Growth Phases and Growing Degree Days

Emergence of the *L. ochroleucus* plants occurred when accumulated temperatures above 0° C reached from approximately 135 to 145 GDD. The duration of the linear growth phase in GDD was approximately 460, meaning that approximately 460 GDD accumulated between emergence and the reproductive/storage phase. The reproductive/storage phase commenced when the heat unit accumulation reached approximately 600 GDD. The above values were not based on statistical theory but were merely descriptive. However, the GDD values determined for the phenophases of *L. ochroleucus* should be useful in the approximation of the timing and duration of the vegetative growth phase, assuming temperature was the dominant factor controlling development.

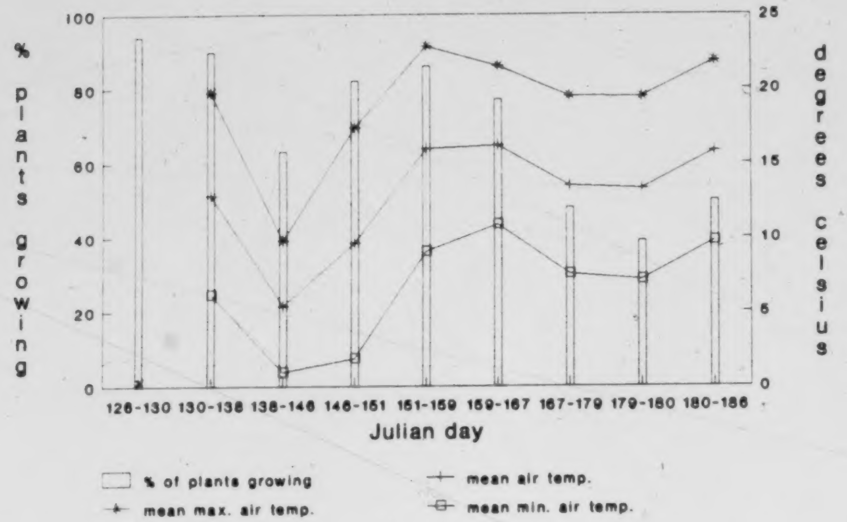
5.3.3 Temperature and Growth Rate

5.3.3.1 Results

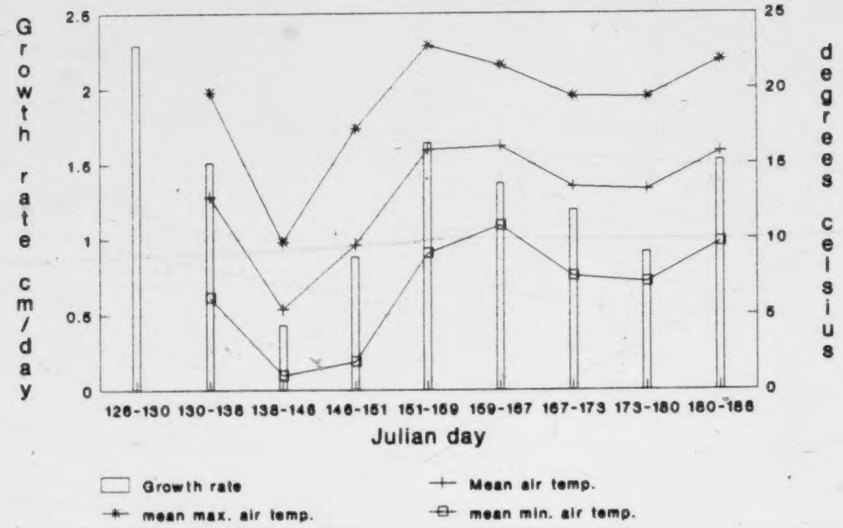
The proportion of plants growing and their growth rates tracked ambient thermal changes during the study period (Figures 5.4 and 5.5). *L. ochroleucus* plants will exhibit temperatures that deviate from ambient conditions, however this deviation was dampened due to the presence of the deciduous tree canopy. Since ambient temperature is the most commonly measured meteorological variable, it was used rather than tissue temperature in the investigation of *L. ochroleucus* growth/temperature relationships. Soil temperature was used as a direct measure of root temperature.

There are statistically significant and relatively high positive correlations between growth rate and air temperature variables, and to a lesser degree soil temperature variables, during the linear growth phase (Table 5.1). The proportion of plants growing also had a significant and high positive correlation with air temperature variables during the linear growth phase (Table 5.1).

During the reproductive/storage phase, temperature variables had no significant relationship with growth rate (Table 5.1). However, the proportion of plants growing had statistically significant correlations with temperature variables during the reproductive/storage phase (Table 5.1). Although highly significant relationships between temperature variables and the proportion of plants growing during the reproductive/storage phase exist, the vegetative growth phase is the focus for analysis because 80% of *L. ochroleucus* production

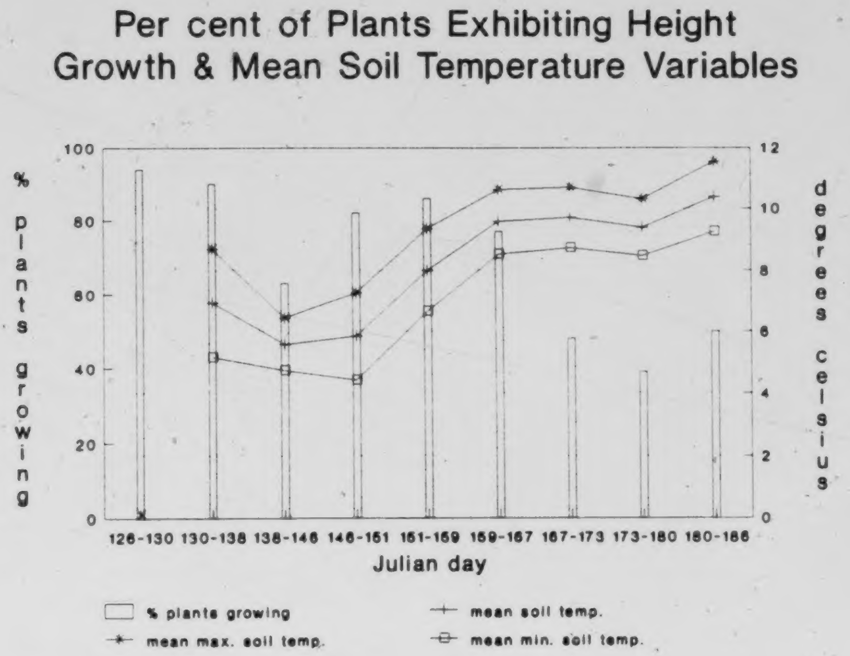


Per cent of Plants Exhibiting Height Growth & Mean Air Temperature Variables

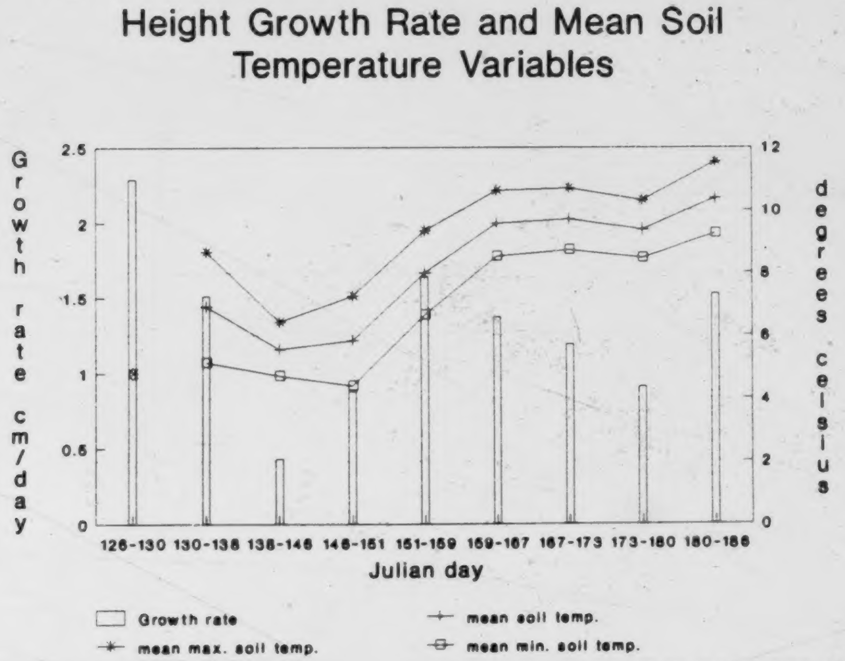


Height Growth Rate and Mean Air Temperature Variables

Figure 5.4 The relationship between the proportion of plants growing, their growth rates and air temperature. (Julian day 126 = 6 May)



Per cent of Plants Exhibiting Height Growth & Mean Soil Temperature Variables



Height Growth Rate and Mean Soil Temperature Variables

Figure 5.5 The proportion of plants growing and their growth rates plotted against soil temperature. (J. Day 126 = 6 May)

Table 5.1. Correlation of environmental factors with the per cent of *L. ochroleucus* plants exhibiting height growth and their height growth rates during the linear and the reproductive/storage (rep.) growth phases, and both phases grouped. All relationships are statistically significant ($P < 0.05$). Non significant relationships were not shown.

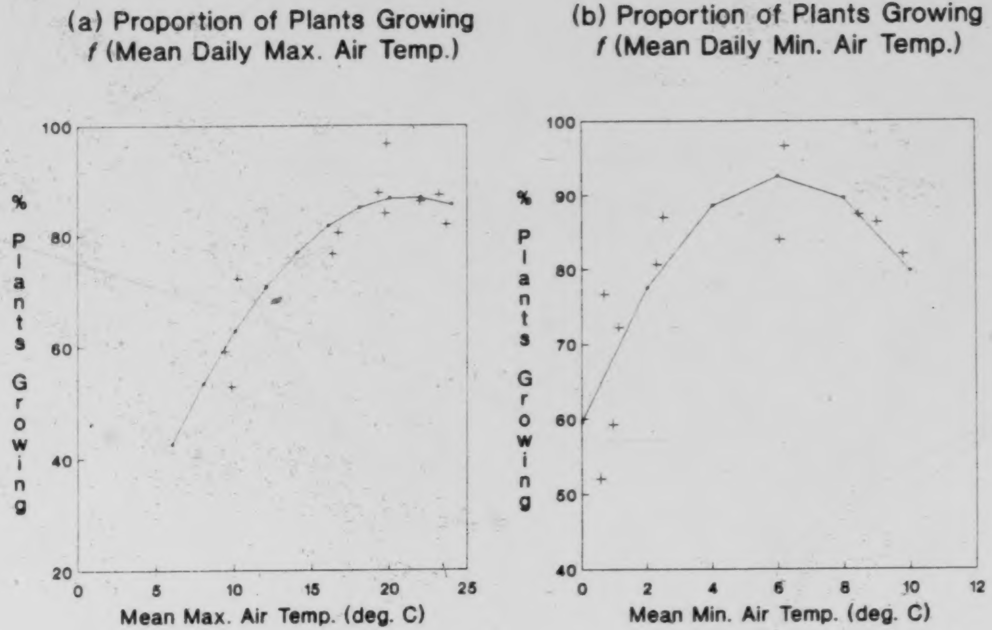
Environmental Factors (Avg. daily temp. variables)	Growth Rate			% Plants Growing		
	Phases			Phases		
	linear	rep.	both	linear	rep.	both
Max. Air Temp.	0.55	-	0.37	0.82	0.58	0.37
Min. Air Temp.	0.52	-	0.10	0.63	0.82	0.10
Mean Air Temp.	0.55	-	0.26	0.77	0.75	0.26
Max. Soil Temp.	0.34	-	0.16	0.63	0.16	-
Min. Soil Temp.	0.23	-	0.10	0.08	-0.32	-0.40
Mean Soil Temp.	0.47	-	0.17	0.59	-0.20	-0.30
Heat units(>0°C)	0.52	-	0.38	0.63	0.86	0.32

occurred during this phase.

The change in the proportion of *L. ochroleucus* plants growing had a distinct parabolic response to air temperature variables (Figure 5.6). The proportion of plants growing increased as the average maximum, minimum, and mean temperatures increased within the temperature ranges of 5° to 19° C, 0° to 6° C and 4° to 13° C, respectively (Figure 5.6a, b, c). The increase of *L. ochroleucus* growth rate with average mean daily temperature has a Q_{10} of 2.56 which indicates that its growth rate is a chemically controlled process. Additional increase in these temperature variables resulted in a reduction in the proportion of plants growing. Similarly, this parabolic response curve was exhibited by growth rate in response to average daily minimum air temperatures (Figure 5.7b). In contrast, there was a nearly linear growth rate increase of *L. ochroleucus* in response to average daily maximum and mean air temperatures (Figure 5.7a, c).

The proportion of plants growing and their growth rates exhibited a parabolic response to average maximum and mean soil temperatures (Figure 5.8a, c and 5.9 a, c). In contrast, *L. ochroleucus* plants exhibited an exponential growth response to average minimum soil temperature (Figure 5.8b).

It was difficult to separate the effects that the different temperature variables had on the proportion of plants growing and growth rate because they varied together even though their relative amplitudes changed. The optimal combination of temperature conditions defined by the models were not independent because the temperature variables were significantly correlated. Therefore, the temperature variables worked in combination affecting plant growth.


(a) Proportion of Plants Growing *f* (Mean Daily Max. Air Temp.)

(b) Proportion of Plants Growing *f* (Mean Daily Min. Air Temp.)

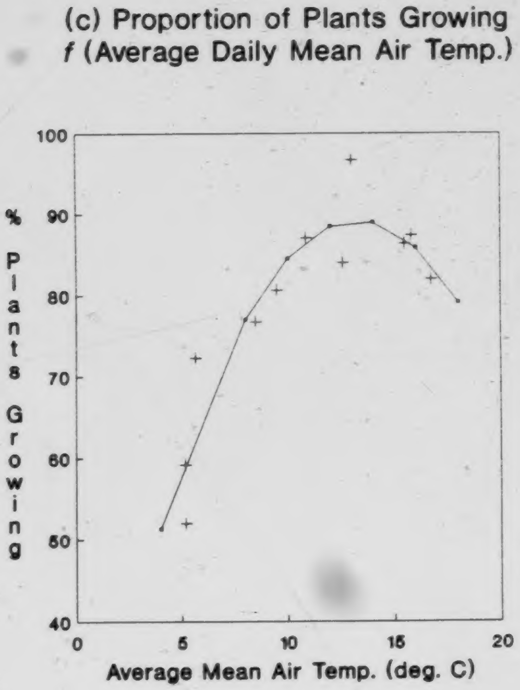
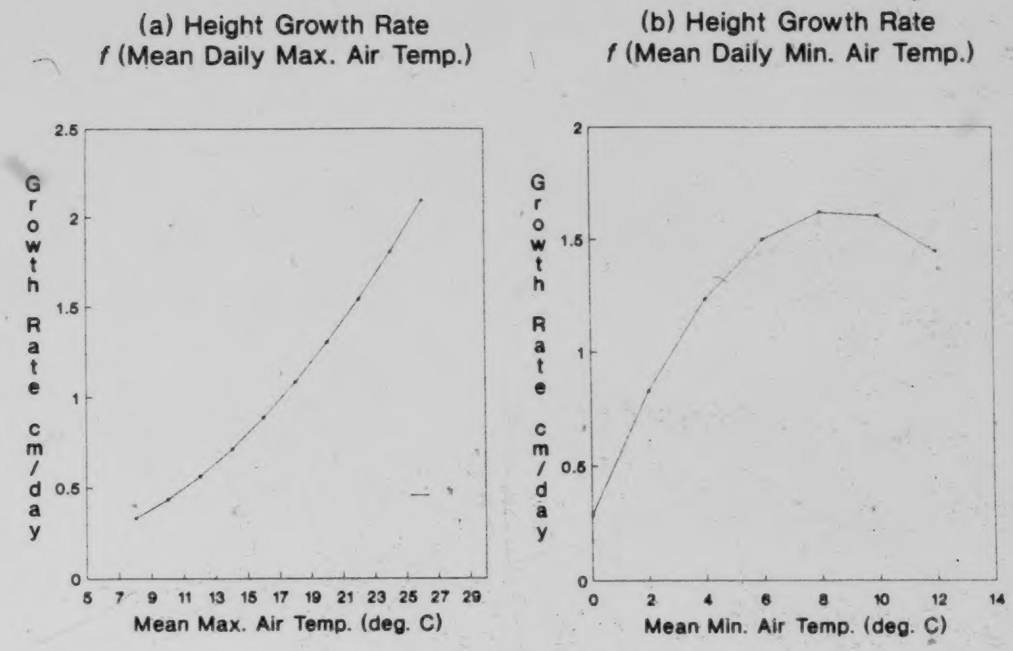

(c) Proportion of Plants Growing *f* (Average Daily Mean Air Temp.)

Figure 5.6 Curvilinear regression models which represent the relationship between the proportion of *L. ochroleucus* plants growing and daily air temperature, MWRS, 6 May to 8 June, 1989.


(a) Height Growth Rate
f (Mean Daily Max. Air Temp.)

(b) Height Growth Rate
f (Mean Daily Min. Air Temp.)

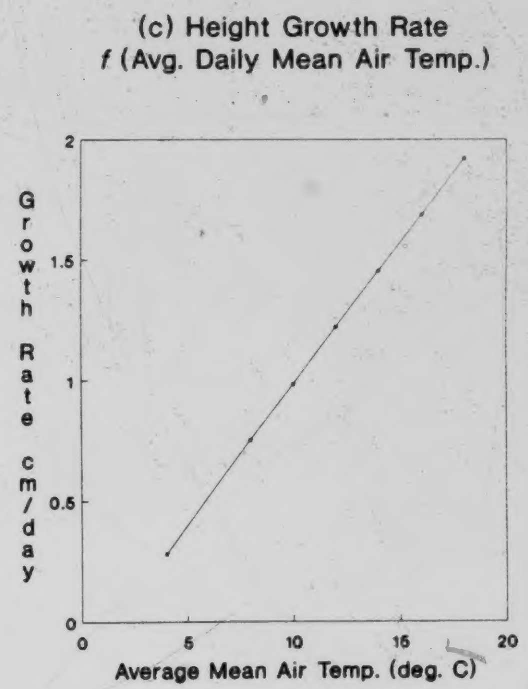
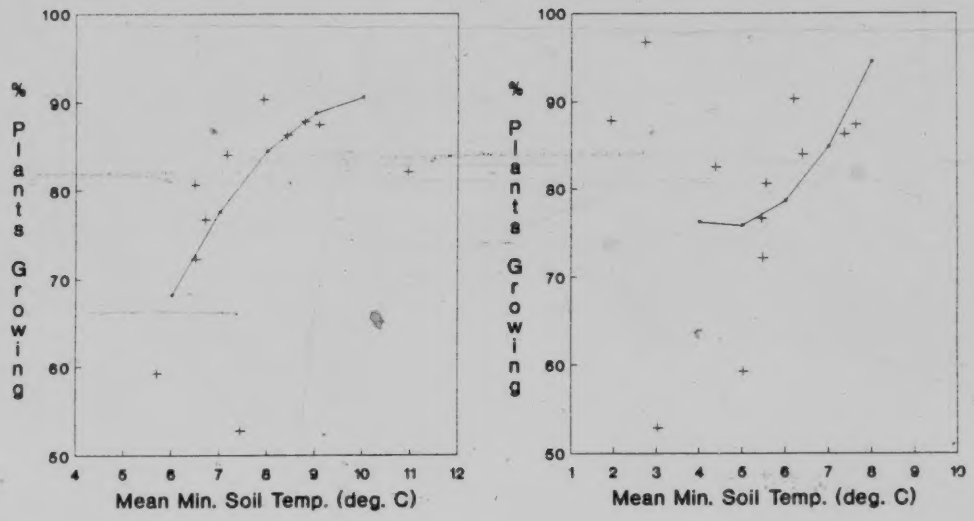

(c) Height Growth Rate
f (Avg. Daily Mean Air Temp.)

Figure 5.7 Regression models which represent the relationship between *L. ochroleucus* growth rate and air temperature, MWRS, 6 May to 8 June, 1989. Supplementary data for the models are in Appendix II.

(a) Proportion of Plants Growing
f (Mean Daily Max. Soil Temp.)

(b) Proportion of Plants Growing
f (Mean Daily Min. Soil Temp.)



(c) Proportion of Plants Growing
f (Average Daily Mean Soil Temp.)

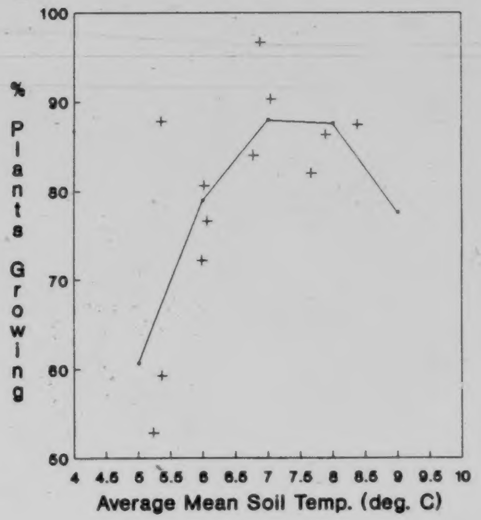
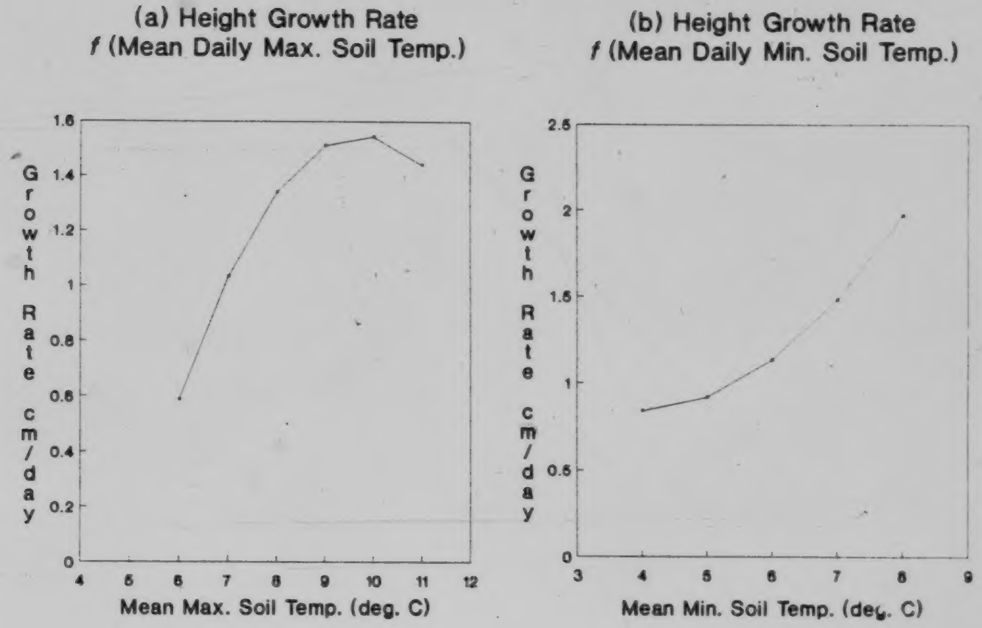


Figure 5.8 Regression models which represent the relationship between the proportion of *L. ochroleucus* plants exhibiting height growth and soil temperature, MWRS, 6 May to 8 June, 1989.



(a) Height Growth Rate
f (Mean Daily Max. Soil Temp.)

(b) Height Growth Rate
f (Mean Daily Min. Soil Temp.)

(c) Height Growth Rate
f (Avg. Daily Mean Soil Temp.)

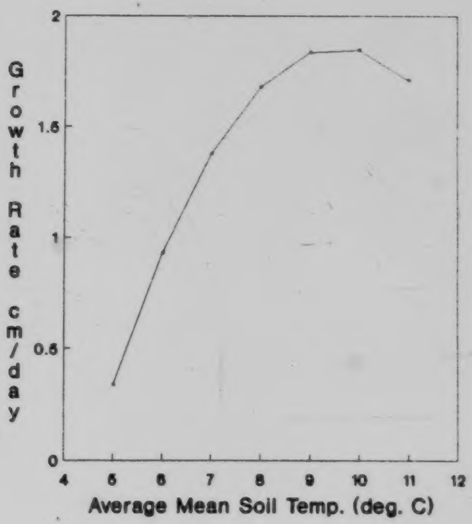


Figure 5.9 Regression models which represent the relationship between *L. ochroleucus* growth rate and soil temperature, MWRS, 6 May to 8 June, 1989. Supplementary data for the models are in Appendix II.

5.3.3.2 Discussion

The growth processes influenced most strongly by temperature, and thus requiring a suitable temperature regime, include chemical reactions, gas solubility, mineral absorption, and water uptake (Treshow, 1970). Since plant development is the end result (integral) of a complex series of biochemical processes, each affected by temperature, it follows that the rate of growth and development of the plants as a whole is dependent on temperature (Landsberg, 1975). A quote from Berry and Raison (1981) helps summarize the important integrated component processes affecting growth:

> Raw materials for growth are the result of photosynthesis, ion uptake and water absorption. These materials are transported and partitioned to the various growing points of the plant. Respiration is required to enable active uptake and transport process; to drive the primary biosynthetic reactions forming proteins, nucleic acids, lipids, and carbohydrates needed for growth, and to maintain the essential life processes of the plant. Normal growth is dependent on the integrated functioning of these processes at an appropriate rate. ...the storage of photosynthate or nutrients may buffer short-term imbalances, but these inputs must be balanced over the long term.

Different temperatures lead to quantitative differences in plant growth as a result of the different rates at which physiological processes proceed in response to temperature (Landsberg, 1975). Every physiological function has temperature limits, above and below which the function ceases (Treshow, 1970). As well, every physiological function has an optimum temperature at which reactions proceed at an optimum rate (Treshow, 1970). Plant processes such as growth which integrate many individual metabolic components are often approximately linearly related to temperature over a wide range of normal temperatures (Jones 1983; Berry and Raison, 1981). An optimum and subsequent decline in the rate of physiological processes is reached at high temperatures (Jones, 1983, Berry and Raison, 1981).

The linear part of the proportion of plants growing and the growth rate plant response curves (Figures 5.6 and 5.7) can be explained by the effects of temperature on the rates of chemical reactions (Went, 1953; Wang 1967; Landsberg, 1975; Berry and Raison, 1981; Larcher, 1983; Jones, 1983; Salisbury and Ross, 1985). At lower temperatures the capacities of all reactions decline according to their individual temperature coefficients (Berry and Raison, 1981). Since the growth of a plant over any given period represents the integrated balance between assimilation and respiration, the temperature sensitivity of these processes may be the key to understanding *L. ochroleucus* growth. In order for a plant to grow, it must have a positive energy balance, that is, it must have energy in excess of that needed for maintenance of existing tissue. At lower temperatures, the proportion of *L. ochroleucus* plants growing and their growth rates were reduced, due to lower rates of photosynthesis and respiration. Reduced reaction rates within these biochemical pathways result in less available chemical energy for ion uptake, osmotic work, and primary biosynthetic reactions, which all require more energy at lower temperatures. Reduced respiration rate would be especially important during the early spring when assimilates accumulated from the previous growing season are utilized for growth and tissue maintenance. With rising temperature, the rates of photosynthesis and respiration increase which results in more available chemical energy for metabolic processes and growth. In addition, there is evidence that at lower temperatures plants store a larger proportion of sugars and carbohydrates rather than metabolizing these substances for new tissue production. (Went, 1953; Warren-Wilson, 1966; Etherington, 1975; Berry and Raison, 1981; Nobel, 1983; Larcher, 1983). These substances may be metabolized as temperatures become more favourable with the chemical energy being utilized in maintenance and growth. The effect of this would be the suppression of growth at lower temperatures due to assimilate storage with subsequent growth increases as temperatures rise.

The linear portion of the plant response to air temperature curves may be explained by the effects of temperature on the rates of chemical reactions and the increased storage of sugars and carbohydrates at lower temperatures. This, however, does not adequately explain the progressive decline in the proportion of plants growing and their growth rates as the temperature variables approach the "optimum" for these processes and then the eventual change in sign of the relationship above the temperature "optimum". The increase in the proportion of plants growing up to the "optimal" with a subsequent decline is evident in the models for all air temperature variables (Figure 5.6). This pattern, however, was only exhibited in the growth rate response model when mean minimum air temperature was the independent variable (Figure 5.7b).

Temperature stimulation of competing reactions can partly explain the reduction in the per cent of plants growing near and subsequent to the "optimum" temperature. The rate of both photorespiration and dark respiration increase faster with temperature than does photosynthesis (Berry and Raison, 981). Photorespiration is directly linked to the rate of photosynthesis because of its dependence on the latter for the provision of substrate (ribulose bisphosphate) (Larcher, 1983). Photorespiration quickly oxidizes the glycolic acid produced by photosynthesis to CO_2 and H_2O without the production of any high energy compounds such as ATP (Meyer et al., 1973). As much as 30% of the photosynthetically fixed carbon may be "recycled" to CO_2 with the energy used to fix it wasted (Ray, 1972). Unlike photorespiration dark respiration produces chemical energy by the oxidation of organic compounds. This chemical energy is used for ion uptake, osmotic work, and primary biosynthetic reactions associated with growth and maintenance of plant cells. Several researchers have separated dark respiration into growth and maintenance components on the basis that growth respiration provides energy for growth and synthesis of new cell constituents and maintenance respiration which supports the life functions of the plant (Thornley, 1970; Topewalla and Sinclair, 1971;

Jones, 1983). Maintenance respiration is assumed to be proportional to dry weight and strongly temperature sensitive while growth respiration is directly dependent on photosynthesis and insensitive to temperature (Jones, 1983; Berry and Raison, 1981). Although there is no biochemical distinction between this division (Jones, 1983) temperature-dependent losses would be restricted to that portion of respiration associated with maintenance (Berry and Raison, 1981).

Respiration is considerably more tolerant of high temperatures than are photosynthetic reactions of the same plant (Bjorkman, 1975). Photosynthesis is itself one of the most responsive of plant processes to temperature (Berry and Raison, 1981). Berry and Raison (1981) explain that besides the photorespiration/photosynthesis ratio increasing with temperature, the capacity of photosynthetic membranes for electron transport is decreased. This results in lower photosynthesis rates at higher temperatures. The effect of respiration and photorespiration increasing faster with temperature than photosynthesis coupled with the decreasing capacity of photosynthetic membranes for electron transport at higher temperatures, may be involved in reducing the proportion of *L. ochroleucus* plants growing at the higher temperatures encountered during the study. At these higher temperatures the *L. ochroleucus* plants that had energy reserves too low to buffer the increased rate of reserve energy utilization, ceased height growth. The growth rates of the remaining plants, however, responded linearly to average daily maximum and mean temperatures, possibly due to their having large enough energy reserves to buffer the affects of increased maintenance respiration at higher temperatures. Growth rates of plants declined at the higher average minimum air temperatures encountered during the study.

Minimum temperatures usually occur just before sunrise and thus are representative of the thermal regime at night. The high average minimum daily temperatures encountered during the study may reduce growth due to a relatively high rate of dark respiration during the night when photosynthates are not produced. Whyte (1960) reported that for *Vicia sativa* (same family as *L. ochroleucus*) an increase in night temperature from 15° C to 21° C significantly reduces above ground dry weight and nitrogen content. High day temperatures favour rapid photosynthesis and low night temperatures reduce (maintenance) respiration to a low level, so the photosynthate produced during the day is conserved (Daubenmire, 1974). The proportion of plants growing and growth rate of *L. ochroleucus* had a parabolic response to average minimum daily air temperature (Figures 5.6 and 5.7). The decline in the proportion of plants growing and growth rate after the optimum response to average minimum air temperature may be due to increased maintenance respiration at higher night temperatures.

Although correlations between net photosynthesis rates measured over short periods and biomass yield are not high (Heichel and Musgrave, 1969; Evans and Dunstone, 1970; Charls-Edwards, 1971; Rhodes, 1972), net photosynthesis is the source of carbon for the synthesis of all organic compounds (Larcher, 1983). Based on a literature survey Downton and Tregunna (1968) concluded that plants with photorespiration have optima net photosynthesis within the range 10° to 25° C. Larcher (1983) reported that the optimum temperature for net photosynthesis of spring flowering perennials is from 10° to 20° C. The greatest proportion of *L. ochroleucus* plants growing occurred when average daily maximum and mean temperatures were within this range. Most likely the largest proportion of plants were growing when net photosynthesis was highest.

The proportion of *L. ochroleucus* plants growing and their growth rates were lower at cooler soil temperatures (Figure 5.8 and 5.9). This could be related to low air temperatures associated with low soil temperatures, both reducing the rate of biochemical reactions and thus inhibiting growth. In addition, lower soil temperatures could be affecting nutrient or water uptake.

Relatively low soil temperatures can significantly reduce water uptake, particularly passive absorption, even when soil water is abundant (Threshow, 1970). Reduced water absorption at relatively low soil temperatures is due primarily to water viscosity increase and reduced permeability of protoplasm (Daubenmire, 1974; Treshow, 1970; Larcher, 1983). The viscosity of water doubles as temperatures drop from 25° to 0° C (Treshow, 1970). Chilling the soil increases water viscosity, thus reducing the absorptive capacity of the roots to the extent of causing wilting (Daubenmire, 1974). After a review of the literature on growth and water deficits Etherington (1975) indicated that water deficits can reduce photosynthesis, net assimilation rate, relative growth rate, cell enlargement and leaf elongation. He also indicated that tolerances to water deficits are species-specific. Larcher (1983) stated that temperate zone species that began development early were, as a rule, less hampered by the effect of low soil temperatures on water uptake than species developing later in the season. *L. ochroleucus*, being an early spring developing species, probably has adaptations which mitigate the water deficit problems associated with cool soil temperatures.

Ion uptake is reduced at lower soil temperatures partially because: (1) the root's metabolic rate declines which reduces the available energy needed for active uptake and transport; and (2) the viscosity of the soil solution increases, thus slowing the movement of ions to the roots (Glass, 1989). At temperatures of 5 to 10° C the importance of temperature limitations on nutrient uptake might be considerable (Glass, 1989). At MWRS during the linear growth phase of *L. ochroleucus* average daily soil temperatures did not rise above 10° C. In fact, the increase in the proportion of plants growing and growth rate slowed and subsequently decreased at average mean and maximum daily soil temperatures greater than 9° C (Figure 5.8 and 5.9). Temperature acclimation to ion uptake at lower temperatures tends to make the process independent of temperature (Clarkson and Deane-Drumond, 1980). During the early spring, the growth of *L. ochroleucus* plants at MWRS were acclimated to a soil temperature range below approximately 12° C.

The reduction in the proportion of *L. ochroleucus* plants growing and their growth rates at higher soil temperatures could be due to a reduction of assimilates available for use in shoot growth by the increased maintenance respiration of roots at higher temperatures. Respiratory losses of carbon by roots can represent a significant fraction of whole-plant carbon usage (Sauerbeck and Johnen, 1977; Lambers, 1985; Martin and Kemp, 1986; Jairo and Nobel, 1989). As root temperatures increase they use a greater proportion of assimilates in maintenance respiration and shoot growth can be reduced (Landsberg, 1975). It appears that root growth at the expense of shoot growth can be stimulated at low or high soil temperatures with optimum shoot growth occurring between the two (Davidson, 1969b; Nielsen et al., 1960a, b; Nielson and Humphries, 1966; Berry and Raison, 1981). *L. ochroleucus* had this response in that shoot growth was reduced at both the high and low soil temperatures encountered during the study. Shoot temperature, however, was influencing growth in cooperation with root temperatures. In experiments where root temperatures were varied while shoot temperatures were held constant and near optimal, there were distinct "optimal root temperatures" occurring between 20° and 30° C for temperate species, where shoot growth was maximal and root/shoot ratio was minimal (Davidson, 1969b). *L. ochroleucus* would probably have lower optimal root temperatures than Davidson (1969b) indicates for temperate species because it exhibited a decrease in growth rate at temperatures greater than approximately 10° C. After reviewing the literature on the effects of soil temperature on plant growth, Nielson and Humphries (1966) concluded that optimum root temperature for any species is not fixed but dependent on shoot temperature, plant age and season of growth.

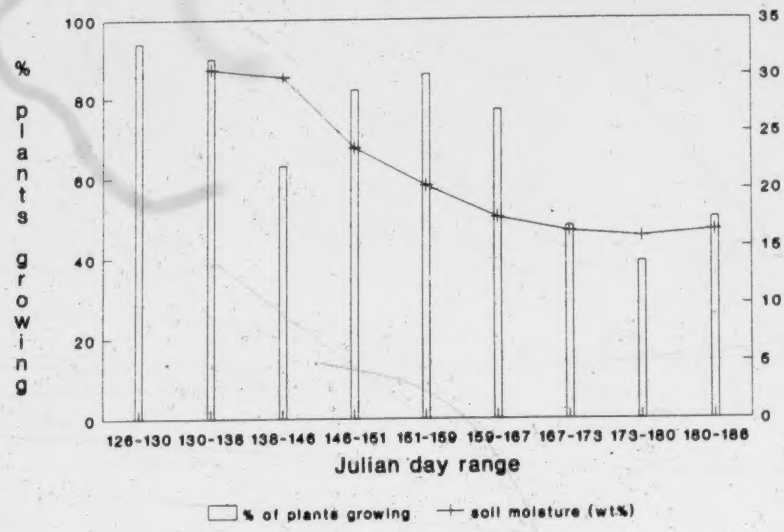
5.3.4 Soil Moisture and *Lathyrus ochroleucus* Growth

Low soil moisture and high transpiration rates can cause plant water deficits (Baier, 1965; Etherington, 1975; Salisbury and Ross, 1983; Crawley, 1986). Plant water deficits affect all the physiological functions of the plant, ranging from primary biochemical processes to the overall reduction of growth and development (Bradford and Hsiao, 1982; Hanson and Hitz, 1982; Morgan, 1984). Plants withdraw water from the soil in response to the water vapour deficit gradient between the leaf and the surrounding air (Salisbury and Ross, 1985). This, however, occurs only as long as the water potential of the plant's fine roots is more negative than that of the soil solution (Larcher, 1983). If water lost from transpiration is not replaced by root absorption then the plant experiences a water deficit.

Soil moisture content was high in the early spring (Julian day 130) after snowmelt and spring rains, but slowly decreased during the study period (Figure 5.10). The growth rate of *L. ochroleucus* did not appear to be strongly affected by water deficits resulting from low soil moisture content. Soil moisture content accounted for a relatively small per cent of the variability in the proportion of plants growing and an even smaller amount of the variability in growth rate. During the vegetative (linear) phase, soil moisture had no significant effect on the per cent of plants growing and only accounted for 0.64% of the variability in growth rate (P=0.05). The negative correlation between growth rate and soil moisture content during the linear growth phase was small (r=-0.08). Growth rate increased with seasonal heating while soil moisture decreased from its post-snowmelt high with increasing evapotranspiration (caused in part by seasonal warming).

Although 1989 was a relatively wet year (Atmospheric Environment Service, personal comm.), the Boreal and Aspen Parkland Ecozones generally do not have water deficits in the spring (Laycock, 1967). In these ecozones it is unlikely that in a "normal" year soil moisture

Per cent of Plants Exhibiting Height Growth and Soil Moisture



Height Growth Rate and Soil Moisture

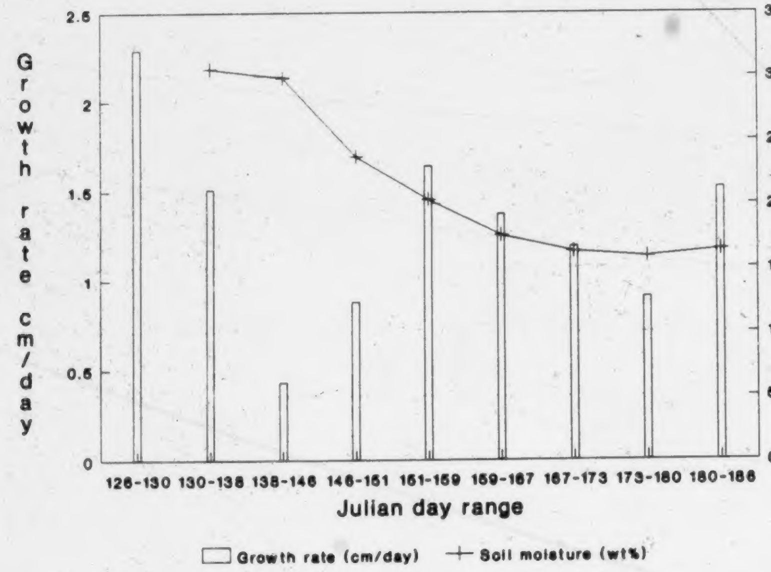


Figure 5.10 Relationship between *L. ochroleucus* growth and soil moisture.

would be limiting to the spring growth of *L. ochroleucus*.

5.3.5 Productivity of *Lathyrus ochroleucus*

5.3.5.1 Results

A second degree curvilinear regression model can be used to explain the relationship between *L. ochroleucus* height and weight (Figure 5.11). Average height is converted to oven dry weight with the use of a second degree polynomial equation (Figure 5.11).

$$\text{odwt} = -0.035518 + 0.0055726 * \text{ht} + 0.00010757 * \text{ht}^2 \qquad (3)$$

where: odwt = oven-dry weight in g
ht = plant height in cm

The average density of *L. ochroleucus* in the aspen-dominated forest in the study area was 10.08 plants m^{-2} (n=50, std=8.482). During the linear growth phase L. ochroleucus produced 25.6 kg ha^{-1} fresh weight or 4.2 g m^{-2} dry weight (Figure 5.12a). The average production rate during the linear growth phase was calculated as 0.192 g m^{-2} d^{-1} dry weight or 1.75 kg ha^{-1} d^{-1} fresh weight (Figure 5.12b).

A second degree curvilinear equation was developed to predict plant height from accumulated heat units (base temp. = 0° C). The equation had the following form:

$$\text{ht} = -35.45851214 + (0.274603 * \text{GDD}) + (-0.000239 * \text{GDD}^2) \qquad (4)$$

where:
ht = plant height in cm
GDD = heat unit summation > 0° C
r^2 = 0.415074
F = 449.54

This equation is based on the height of the individual plant (dependent variable). The high degree of variability among the heights of these individuals causes the error associated with prediction to be large. The high degree of variability in height among the individual plants is represented by the relatively low r^2 value (r^2 = 0.415084). The purpose

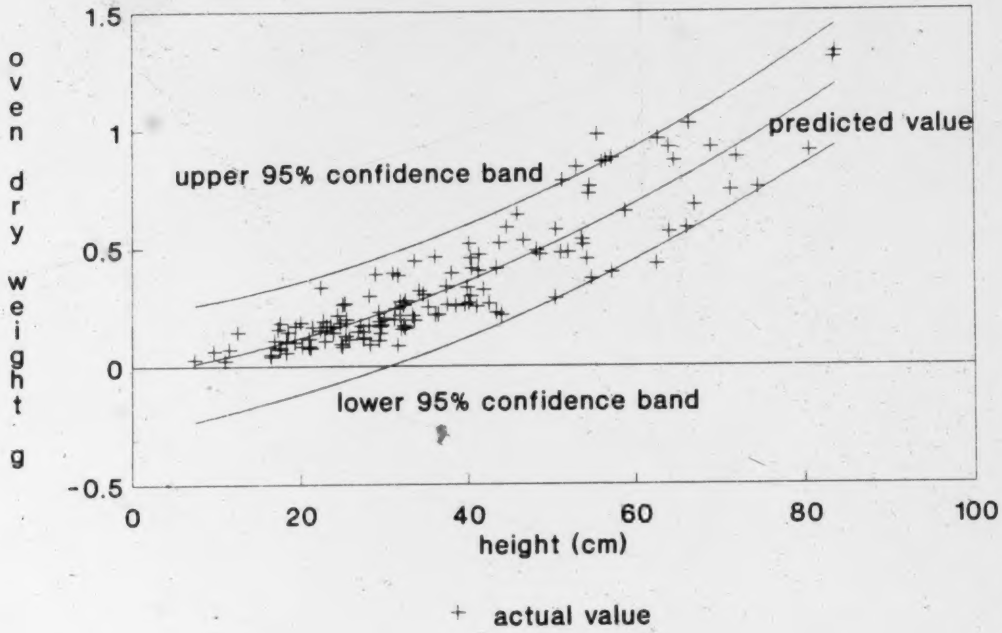
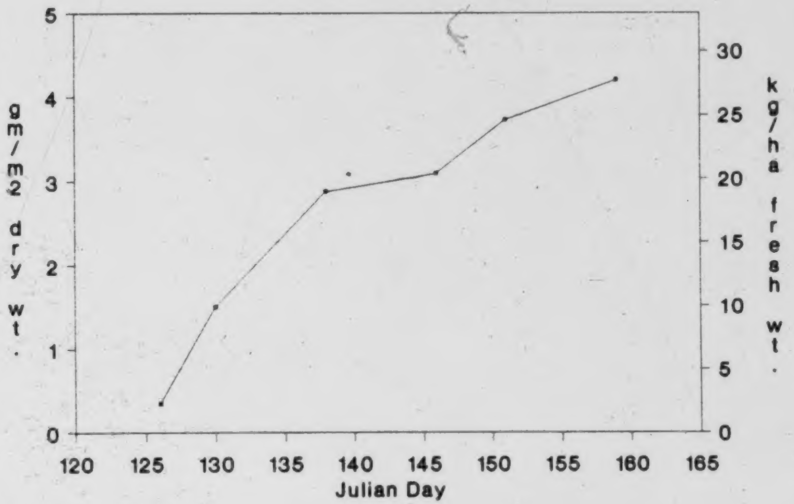


Figure 5.11 Regression model that uses *L. ochroleucus* plant height (cm) to predict plant oven dry weight (g) (r^2=0.82).

(a) L. ochroleocus Net Production in Aspen Dominated Forest at MWRS, 1989



(b) L. ochroleucus Net Production Rate in Aspen Dominated Forest at MWRS, 1989

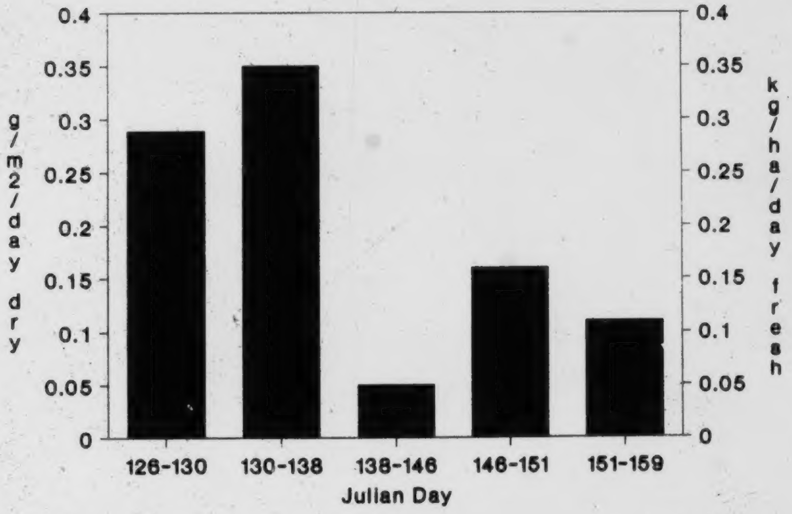


Figure 5.12 (a) *L. ochroleucus* yield per unit area during its linear growth phase in aspen-dominated forest at MWRS, 6 May to 8 June, 1989. (b) *L. ochroleucus* production rate per unit area during its linear growth phase in aspen-dominated forest at MWRS, 6 May to 8 June.

of developing an equation is to predict average plant height within any aspen-dominated forest based on heat unit accumulations at the specific site of interest. Since the above model had a relatively large degree of error associated with the prediction of individual plant heights, a model was developed to predict the average plant height at particular sites within aspen-dominated forests.

A second degree polynomial equation was developed to predict average plant height from accumulated heat units (base temp. = 0° C) (Figure 5.13). The equation had the following form:

$$Aht = -36.175803 + (0.280093 * GDD) + (-0.000249 * GDD^2) \quad (5)$$

where:

Aht = average plant height in cm
GDD = heat unit summation > 0° C
r^2 = 0.9307
F = 108.5

5.3.5.2 Discussion

The high r^2 value obtained from equation 5 is the result of using average plant height from each study site as the dependent variable rather than using the heights of the individual shoots (equation 4). When using the average plant height for each site much of the variability among the individuals is lost. This loss of variability causes the models to differ in their values of r^2 and F. However, both regression models are not significantly different with respect to intercept and slope ($P = 0.05$). Therefore, the predicted height values from the two equations (equations 4 and 5) are identical (statistically not different), but the models differ in their assessment of estimate reliability (confidence limits). This is because the confidence limits associated with equation 4 refer to the confidence in the prediction of the height of the individual plant, whereas for equation 5 they refer to the confidence in the prediction of the average plant height. Thus, considering the variability in the heights of the individual plants, it is not surprising that the 95% confidence limits for equation 4 are 3.48

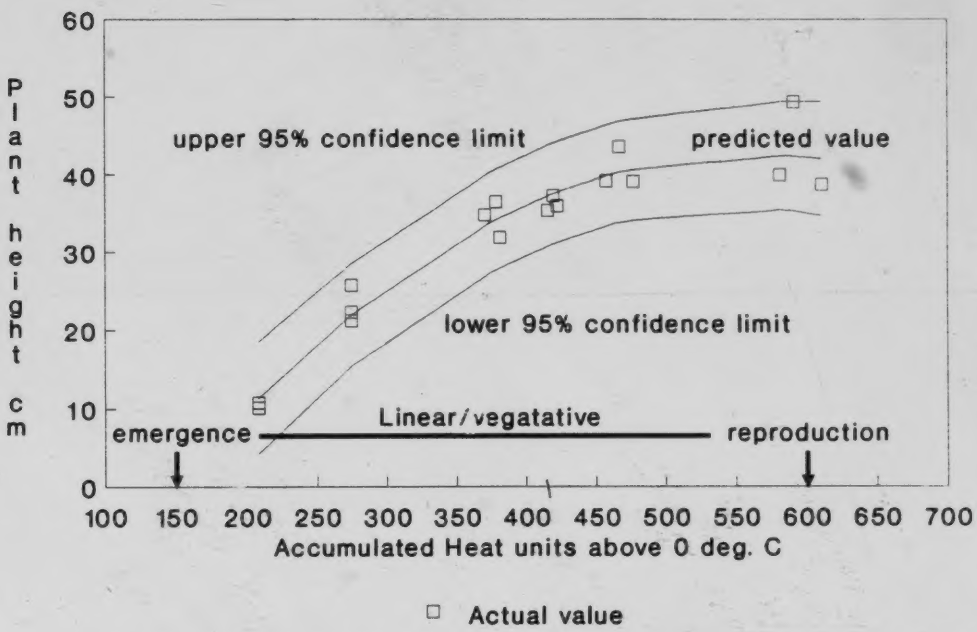


Figure 5.13 Regression model for the prediction of the average height of *L. ochroleucus* plants in aspen-dominated forests by using accumulated heat units above 0° C. This model was developed with data collected at MWRS during 6 May to 8 June, 1989.

times wider than those of equation 5. Variability loss in this case is fine, since it is average plant height at the particular site that is required when height values are used with the site's plant density data to estimate production. Thus, the r^2 value of equation 5 provides a better indication of the confidence in predicting average plant height at a particular site than equation 4 when using heat unit accumulations as the independent variable in second degree polynomial regression.

Accumulated heat units can be used to predict the height of *L. ochroleucus*. Once the height is known the production can be estimated as long as plant density is known. *L. ochroleucus* plant density varies considerably from place to place and most likely between years. Therefore, when predicting production, plant density should be determined for the specific site and year. Other errors associated with estimating forage production are outlined below. The steps in the procedure to determine *L. ochroleucus* production from heat unit summations are as follows.

(1) Determine the accumulated heat units above 0° C (GDD) for the dates that *L. ochroleucus* production estimates are needed.

(2) Use the accumulated heat units in equation 5 to determine average plant height (Aht, in cm).

(3) Average plant height (Aht, in cm) is then used in equation 3 as plant height (ht, in cm) to determine average oven dry weight (Aod wt, in g).

(4) Forage available:

a) dry weight (g m^{-2} or kg ha^{-1}) - go to (6).

b) fresh weight (kg ha^{-1} or g m^{-2}) - go to (5).

(5) fresh weight (kg ha^{-1} or g m^{-2})

a) use Aod wt. in equation 2 to obtain average fresh weight (g).

b) average fresh weight (g) multiplied by density (plants m^{-2}) will give standing crop in kg ha^{-1}.

(6) dry weight (g m^{-2} or kg ha^{-1}) is determined by multiplying plant density (plants m^{-2}) by Aod wt. (g).

The errors associated with this method are due to:

(1) The inherent errors in the regression models themselves.

(2) Data generalization i.e. using average plant height and GGD accumulations based on mean daily temperatures.

(3) The variability in the plant density estimate.

This method was developed, but has not been tested with field data, so interpretation of model results should be made with caution especially if it is applied in plant community types different from the aspen-dominated community described in this study. However, these methods should be useful in estimating *L. ochroleucus* vegetative production in the spring when high quality forage is essential to animals due to their low nutritional status caused by winter energy deficits (weight loss).

5.4 Conclusions

Based on the variability in the growth of *L. ochroleucus* in the three sampling sites at MWRS during the spring and early summer of 1989, it is apparent that mesoclimate had a stronger influence on its growth than microclimate. The mesoclimatic influences of the regional weather patterns were approximately 21 times stronger in their influence on *L. ochroleucus* growth than the microclimatic differences among sample sites. This suggests that official meteorological records which reflect mesoscale climate may be usefully applied in evaluating *L. ochroleucus* growth.

The increase of *L. ochroleucus* growth rate with average mean daily temperature has a Q_{10} of 2.56 which indicates that its growth rate is a chemically controlled process. Processes with Q_{10} values of 1.3 to 1.5 are physically controlled processes (i.e. gas or water diffusion) where as most biochemical and chemical reactions have Q_{10} > two (Noble, 1983). The linear growth response of *L. ochroleucus* to increasing temperatures up to the "optimal" may be explained by the effects of temperature on the rates of chemical reactions and the increased tendency of plants to store larger quantities of sugars and carbohydrates at lower temperatures. The quantity of energy reserves a plant has will influence its response to high temperatures. The energy consumptive processes of maintenance respiration and photorespiration increase faster with temperature than does photosynthesis. Thus, at high temperatures energy is used at a faster rate than it is produced. *L. ochroleucus* plants that had energy reserves too low to buffer this energy loss, ceased to grow in height. Those that did grow, however, responded to average daily maximum and mean temperatures in an almost linear fashion, possibly due to large enough energy reserves to buffer the effects of increased respiration at the higher temperatures. The growth rate of the plants that exhibited a linear growth response to average daily maximum and mean temperatures was reduced at the higher average minimum daily air temperatures encountered during the study. The increased energy reserve utilization caused by increased maintenance respiration at higher night temperatures (higher minimum air temperatures) reduces growth rates by reducing the quantity of carbohydrate reserves available for growth.

L. ochroleucus, an early-spring developing species, has to take up water and ions from cool soils early in its growing season. Although it has probably evolved physiological adaptations to mitigate water or ion uptake problems associated with low soil temperatures, low temperature inhibition of these energy-dependent processes affects its growth. Since low root temperatures favour root growth over shoot growth, *L. ochroleucus* may respond to low temperatures by increasing its root/shoot ratio.

The vegetative growth of *L. ochroleucus* is affected by the temperature regime of both its shoots and roots. The separation of these effects and the determination of its lethal, threshold, and optimum temperature ranges requires controlled environmental experimentation. The temperature regime of this study and its effects on *L. ochroleucus* growth, however, can be considered representative of their relationship in *Populus tremuloides*-dominated forests.

Soil moisture content during the spring and summer of 1989 at MWRS was not a factor limiting the growth of *L. ochroleucus*. It was expected that soil moisture would not limit the growth rate of *L. ochroleucus* during its linear growth phase in a "normal" year in *Populus tremuloides*-dominated forests. This is due to the rarity of soil moisture deficits at this time of year in these forest types.

The quantity of *L. ochroleucus* available for forage in aspen-dominated forests during the spring and early summer can be predicted. The height of *L. ochroleucus* during its linear growth phase in the *Populus tremuloides*-dominated forest in 1989 at MWRS was accurately predicted (Figure 5.13) by using GDD in a second degree polynomial equation (equation 5). With a relatively high degree of accuracy the oven-dry weight of *L. ochroleucus* within the *Populus tremuloides*-dominated forest can be estimated using the average height data from equation 5 in a second degree polynomial equation (equation 3) (Figure 5.11). The biomass estimate or the average *L. ochroleucus* plant in the *Populus tremuloides*-dominated forest can then be multiplied by it's density to obtain dry weight biomass per unit area. Although there are errors associated with this procedure it should be useful in estimating *L. ochroleucus* vegetative standing crop or production in *Populus tremuloides*-dominated forests during the spring.

The production of 25 kg ha^{-1} fresh matter for *L. ochroleucus* in the *Populus tremuloides*-dominated forest at MWRS during the spring and early summer of 1989 suggests it could contribute significantly to forage resources. This is especially true due to its high forage quality (Adams et al., 1986).

Although considerable work is required to understand the influence that environmental factors have on the growth and production of *L. ochroleucus*, this study assists in the understanding of plant responses and in the identification of the mechanisms involved.

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6.0 The Influence of Simulated Grazing on the Growth and Production of Lathyrus ochroleucus.

6.1 Introduction

Grazing can either stimulate or hinder a plant's vegetative growth (Jameson, 1964; Barbour et al., 1980). In nearly all cases when a single species, as opposed to a mixture of species, has been considered, clipping has reduced dry matter yield (Jameson, 1963, 1964). In, general the more frequent and severe the grazing (clipping) the more dry matter yield is depressed (Kennedy, 1950; Hedrick, 1958; Cook et al., 1958; Ellison, 1960; Davis, 1960). Although this evidence indicates that clipping reduces yields, less severe clipping can actually enhance production (Decker et al., 1960; Parsons and Davis, 1960; Kust and Smith, 1961). Davidson and Donald (1958) suggest that the amount of tissue (leaf area) remaining after grazing may be more important than the amount removed.

A plant's response to grazing is dependent on the severity and frequency of tissue removal and its ability to mitigate the effects of partial defoliation. Defoliation of forage plants results in the readjustment of plant metabolism for promotion of new leaf area expansion and re-establishment of photosynthetic capacity (Culvenor, Davidson and Simpson, 1989). The ability of a plant to mitigate the effects of partial defoliation are affected by the following factors:

(1) The quantity of stored energy reserves and structural compounds (Jameson, 1964; Hodgkinson, 1969; Smith and Silva, 1969).

(2) The plant's stage of development (Dent, 1959; Jameson, 1964; Cooper and Watson, 1968; Donart and Cook, 1970).

(3) The type and age of tissue removed (Jameson, 1963, 1964; Hodgkinson, 1974).

(4) The environmental conditions to which the plant is subjected (Jameson, 1963; Davidson and Milthorpe, 1965).

As well, species-specific adaptations have evolved whereby some plants can adjust metabolic processes to mitigate the effects of herbivory (Davidson and Milthorpe, 1966; Ryle and Powell, 1975; Ryle, Powell and

Gordon, 1985; Culvenor, Davidson and Simpson, 1989b).

The amount of regrowth subsequent to clipping depends on the plant's carbohydrate reserve level prior to clipping (Ehara and Macda, 1961; Ward and Blaser, 1961). However, May (1969) indicated that additional carbohydrates above a minimum level did not result in additional growth once the basic requirements had been met. Conversely, Morgan, Sprague and Sullivan (1953) studied the carbohydrate balance of *Trifolium repens* and concluded that only carbohydrates above a certain minimum level were effective as reserve substances for regrowth.

The number, location, and activity of meristems are particularly important limiting factors for the re-establishment of foliage (Richards, 1984). The apical meristem is thought to suppress the growth of lateral buds by the production of auxins (Salisbury and Ross, 1985; Crawley, 1986). Removal of the meristem releases lower buds which may then grow into replacement shoots (Jameson, 1963; Salisbury and Ross, 1985).

For this research, the effects of a clipping treatment (grazing simulation) on the growth and production of *Lathyrus ochroleucus* Hook. were evaluated. *L. ochroleucus* is an important forage species for ungulates (deer, wapiti, and bison) as well as cattle. It is preferentially selected (Blood, 1966; Weatherill and Keith, 1969; Hunt, 1979; Watson et al., 1980) and is utilized much in excess of its availability relative to other forbs (Weatherill and Keith, 1969). *L. ochroleucus* is a decreaser species, sensitive to continued overuse on rangelands (Weatherill and Keith, 1969; Watson et al., 1980; Adams et al., 1986; Smoliak et al., 1988). This is due to its high palatability and nutrient content (Adams et al., 1986). Weatherill and Keith (1969) found that *L. ochroleucus* per cent frequency increased under light cattle grazing intensity and decreased under heavy cattle grazing intensity in Aspen Parkland. Nietfeld (1983) found *L. ochroleucus* composed approximately 12% of the total bites taken by wapiti in the poplar forest at MWRS. Blood (1966) and Hunt (1979) found *L. ochroleucus* made up a significant portion of the rumen contents of wapiti, composing over 50% of the rumen contents in the former study and 4.2% of the summer rumen contents in the later. This study focused on the regrowth of *L. ochroleucus* during the four weeks subsequent to its clipping. The clipping was implemented during the early summer (June 8) when *L. ochroleucus* was most highly utilized (Blood, 1966; Weatherill and Keith, 1969). The response of *L. ochroleucus* to simulated grazing during this time period is an attempt to assess plants sensitivity to defoliation under a temporally realistic grazing regime.

6.1.1 Objectives

The objectives for the study were:

1) To determine if the amount of tissue removed from *L. ochroleucus* affects its growth rate after partial defoliation;

(2) To determine the effects of simulated grazing on the proportion of *L. ochroleucus* plants growing and their growth rates after partial defoliation;

(3) To determine the effect of simulated grazing on the production of *L. ochroleucus*.

6.2 Methods

Three sites were selected to study the affects of simulated grazing on the growth and production of *L. ochroleucus* (Figure 4.3). Each site had an abundance of *L. ochroleucus* and was centred at an existing microclimate station. At each site, 90 to 130 plants were located and marked by placing a T-stake in the ground by the plant.

Lines were etched on the T-stakes to act as a reference point for measuring plant height. The T-stake was pushed into the soil so the etching was at goound level. The height of each plant was measured from May through July at weekly intervals. Height of the plant was determined to the nearest millimetre by measuring the distance from the etching on the T-stake to the highest tip of the plant. If auxiliary buds developed into branches, the length of the shoot from the main stem to the shoot tip was measured. The shoot length was then added to the main stem value to obtain total plant height.

On the 8 June, 1989 (Julian day 159) 66% of the plants from each site were clipped to a height of 25 cm. Since the plants were an average of 44.1 cm tall at the time of clipping an average of approximately 55% of the tissue was removed by clipping. Height of the clipped plants were monitored in the same fashion as the control plants (not-clipped). The clipping height of 25cm was used because below this height access by ungulates is limited due to the protection afforded by the surrounding vegetation. *L. ochroleucus* plants attach themselves to the surrounding vegetation with tendrils which anchor the plants and prevent them from being uprooted by grazing herbivores such as wapiti. The tissue removed was that closest to the apex and thus the youngest. Although young tissue removal is more damaging to the plants regrowth (Harper, 1977), young tissue has a higher protein and nutrient content than that of older tissue, so is preferentially selected by herbivores (Dirzo, 1984; Harper, 1977; Arnold, 1964).

6.2.1 Plant Growth and Parametric Statistics

Growth rate (cm d^{-1}) was calculated by subtracting each plant's height from its previously measured height and dividing by the number of days between the two sampling times:

ht@T2 - ht@T1 / JD@T2 - JD@T1 = GR (1)

Where:

ht@T1 = Plant height at time T1 (cm)
ht@T2 = Plant height at time T2 (cm)
JD@T1 = Julian day at time T1
JD@T2 = Julian day at time T2
GR = Growth rate (cm d^{-1})

Growth rate is a ratio scale measurement and grnerates more information than any other scale of measurement (Norcliffe, 1982) and, where possible, is used in further analysis.

During each sampling interval there were plants that did not grow or exhibited no measurable height growth. This caused the growth rate data to be positively skewed with a relatively large number of plants having a growth rate of 0. To alleviate this problem and permit the use of parametric statistics, the percentage of plants exhibiting measurable growth and their growth rates (cm d^{-1}) were analyzed separately.

The Sharpo-Wilk statistic ($n<51$) or the Kolomogorov D statistic ($n>51$) were used to test the probability ($P < 0.15$) that the data were a random sample from a normal distribution (SAS Institute Inc., 1985). If the data were not normally distributed according to the above mentioned tests, then data transformations were preformed to meet the test's normality requirements. The only variable that required transformation was growth rate. The natural log of growth rate suitably shifted the distribution to allow the use of parametric statistics.

6.2.2 The Effect of the Quantity of Tissue Removed on the Growth Rate of *L. ochroleucus*.

The mean pre-clipping height of the plants was approximately 44 cm, although considerable variation existed (std = 21.23). Since all clipped plants were cut to a height of 25cm from ground level, the pre-clipping height represented the amount of phytomass removed. Thus, the pre-clipping plant height represents the severity of the clipping treatment, with taller plants having more tissue removed than shorter plants. The effect that the severity of simulated grazing had on the proportion of plants growing and growth rate, during the sampling intervals after clipping, was tested using regression analysis. Height before clipping was the independent variable regressed against both the proportion of plants growing and their growth rates.

6.2.3 Differences in *Lathyrus ochroleucus* Growth Rate in the Clipped and Control (not-clipped) Treatments

Significant differences in the proportion of plants growing and growth rate between the clipped and control (not-clipped) treatments were tested using a one way analysis of variance (ANOVA) procedure (SAS Institute Inc., 1985). In the oneway ANOVA tests, per cent of plants growing and growth rate were the dependent variables in two separate tests with the independent variable (treatment) having clipped and control classes. This analysis was performed with all sampling intervals grouped and for each sampling interval separately.

6.2.4 The Effect of Clipping on Production

To more effectively evaluate the effect of clipping on the production of *L. ochroleucus* the growth rate was adjusted for the per cent of plants that had a growth rate of 0. The following formula were used to calculate adjusted growth rate:

$$AGR = MGR \times G\% \times 0.01 \qquad (2)$$

Where:

AGR = adjusted growth rate
MGR = mean growth rate for the site
G% = per cent plants growing at the site

Although the variability in the growth rate of the individual plant was lost, the AGR is the true average rate of growth for a site because it includes the plants that did not grow or had height changes too low to measure in the calculation of average growth rate for the site.

The post average clipping height growth of *L. ochroleucus* in the clipped and control treatments was calculated with the following formula:

$$HtG = AGR \times ND \qquad (3)$$

Where:

HtG = average height growth of individuals at a site.
AGR = adjusted growth rate.
ND = number of days in sampling interval to which AGR applies.

The average height growth was added to the average pre-clipping height for each sampling date for the two treatments. These heights were converted to the average oven-dry weight with the use of a second degree polynomial equation (Chapter 5, Figure 5.10, equation 3). The increase in oven dry weight for each sampling interval and treatment was calculated with the following formula:

$$PR = odwT2 - odwt1 / JDT2 - JDT1 \qquad (4)$$

Where:

$odwT1$ = average oven-dry weight at time T1 (g)
$odwT2$ = average oven-dry weight at time T2 (g)
$JDT1$ = Julian day at time T1
$JDT2$ = Julian day at time T2
PR = Production rate (g $plant^{-1}$ d^{-1})

In range management terminology, production is often expressed as fresh weight. Since *L. ochroleucus* is 83 to 84% water (Makasheva, 1986) the fresh weight was calculated from the oven dry weight by the following formula:

$$\text{Fresh weight (g)} = \frac{\text{oven dry weight(g)} * 100}{16.5} \qquad (5)$$

Once the average weight per plant was calculated it was expressed on an areal basis by multiplying by plant density (plants m^{-2}). Plant density was determined by randomly placing 50 1×1 m quadrats in plant communities that had a tree cover of greater than 40% of which no less than 50% was *Populus tremuloides*. The average density of *L. ochroleucus* in the aspen-dominated forest in the study area was 10.08 plants m^{-2} (n=50, std=8.482). The production rate (PR) was expressed as the increase in dry matter per unit area per unit time (Larcher, 1983). Production rate was expressed on an areal basis in dry ($g\ m^{-2}\ d^{-1}$) and fresh weight ($kg\ ha^{-1}\ d^{-1}$) for both the clipped and control treatments.

6.3 Results

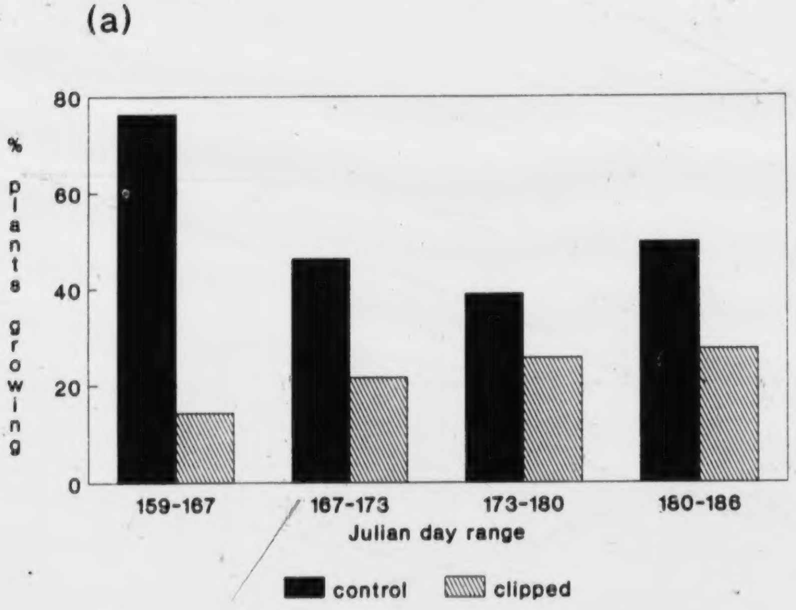
6.3.1 The effect of the quantity of tissue removed from *L. ochroleucus* on its growth rate.

The quantity of tissue removed was greater for larger plants because all were clipped to the same height (25cm). Thus, the pre-clipping height represents the severity of the clipping treatment. Plant height before clipping had no statistically significant relationship with the proportion of plants growing or their growth rates.

6.3.2 The effect of clipping *L. ochroleucus* on the proportion of plants growing, their growth rates and production.

The proportion of plants growing was significantly lower in the clipped than the control treatment during each of the four weekly intervals following clipping (Figure 6.1) (P <0.0001). This difference was especially pronounced during the first two weeks following clipping after which time the proportion of plants growing in the two treatments tended to converge (Figure 6.1a). Fifty seven per cent of the variability in the proportion of plants growing may be explained by the clipping treatment when all sampling intervals are grouped (P < 0.001).

The growth rate of the plants that did grow was significantly lower in the control than in the clipping treatment when all sampling intervals were grouped (Figure 6.1b) (P < 0.001). However, clipping only explained 2.7% of the variation in growth rate after partial



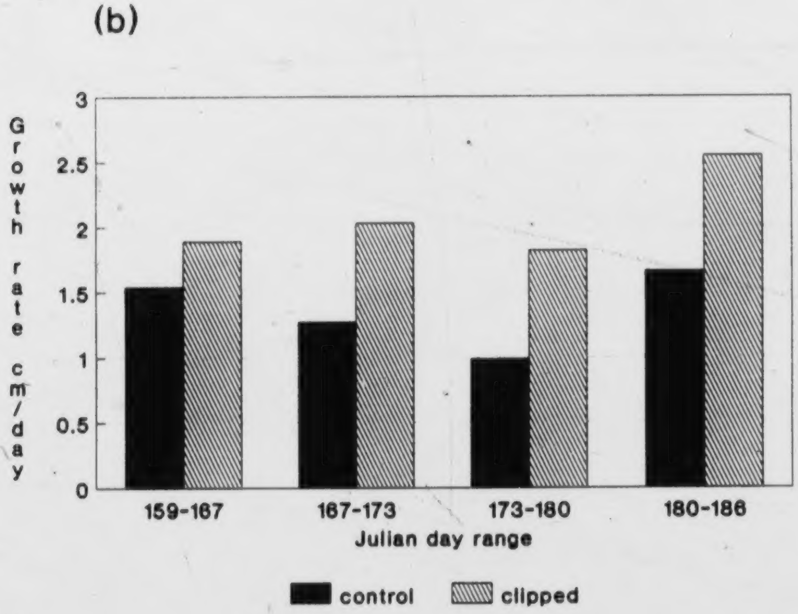


Figure 6.1 (a) Comparison between the per cent of *L. ochroleucus* plants growing after clipping in the control and clipped treatments. (b) Comparison of the growth rates of *L. ochroleucus* plants in the control and clipped treatments subsequent to clipping.

defoliation. When each sampling interval was analyzed separately the growth rate difference between the treatments (clipped and control) was statistically significant only during the first week after clipping (*P*=0.05). This trend, although not statistically, significant continued whereby the clipped plants had higher growth rates than the control plants during the 2nd, 3rd, and 4th weeks after clipping.

Clipping caused fewer plants to grow compared to the control group, but the clipped plants that did grow had higher rates than the control plants. The adjusted growth rate (AGR) represents the combined influence of the proportion of plants growing and their growth rates which in effect is the average rate of *L. ochroleucus* growth for the individual plants at the study sites (Figure 6.2). It is evident that the average post clipping growth rate of the individual plants in the three sites was reduced by the clipping treatment (Figure 6.2). The clipping treatment accounted for 17% of the variability in AGR during the four weeks subsequent to clipping ($P < 0.0409$).

The difference in AGR between treatments resulted in differences in production rate and biomass yield (Figure 6.3). The largest difference in production rate between the treatments occurred during the first week after clipping (Figure 6.3).

6.4 Discussion

The pre-clipping height of *L. ochroleucus* plants represents the severity of the clipping treatment since all plants were clipped to the same height (25cm). Larger plants had a greater proportion of their tissue removed. The severity of clipping as represented by plant size prior to clipping did not influence the rate of regrowth. This is in contrast to the results of Sullivan and Sprague (1953) for *Dactylis glomerata* where pre-clipping plant height was strongly related to regrowth but carbohydrate concentration was not. Harper (1977), however, states that the ability of a plant to recover after defoliation

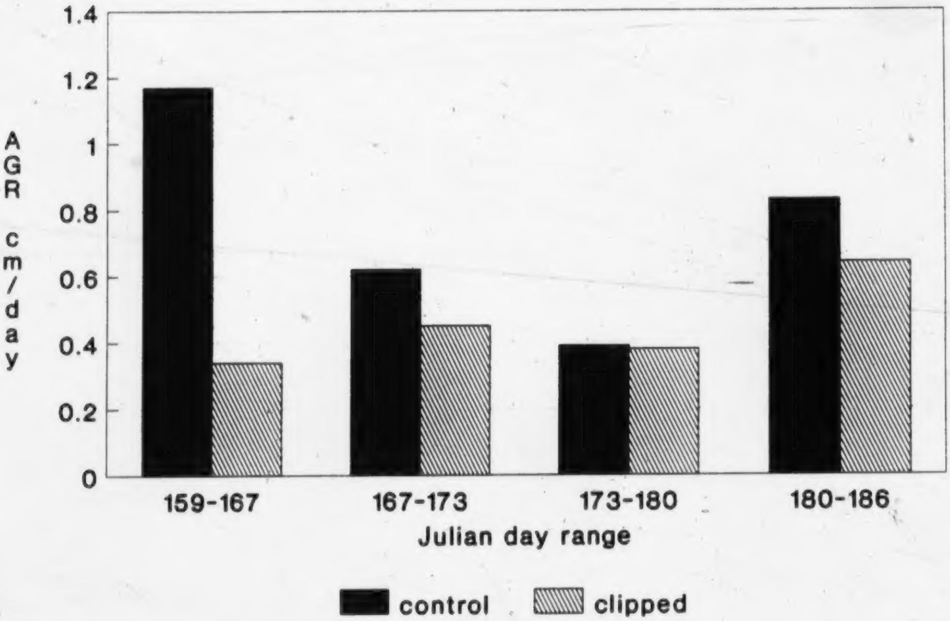


Figure 6.2 Comparison of the adjusted growth rate (AGR) of *L. ochroleucus* plants between the control and clipped treatments. AGR is the growth rate adjusted to account for the proportion of plants that were not growing (see equation 2).

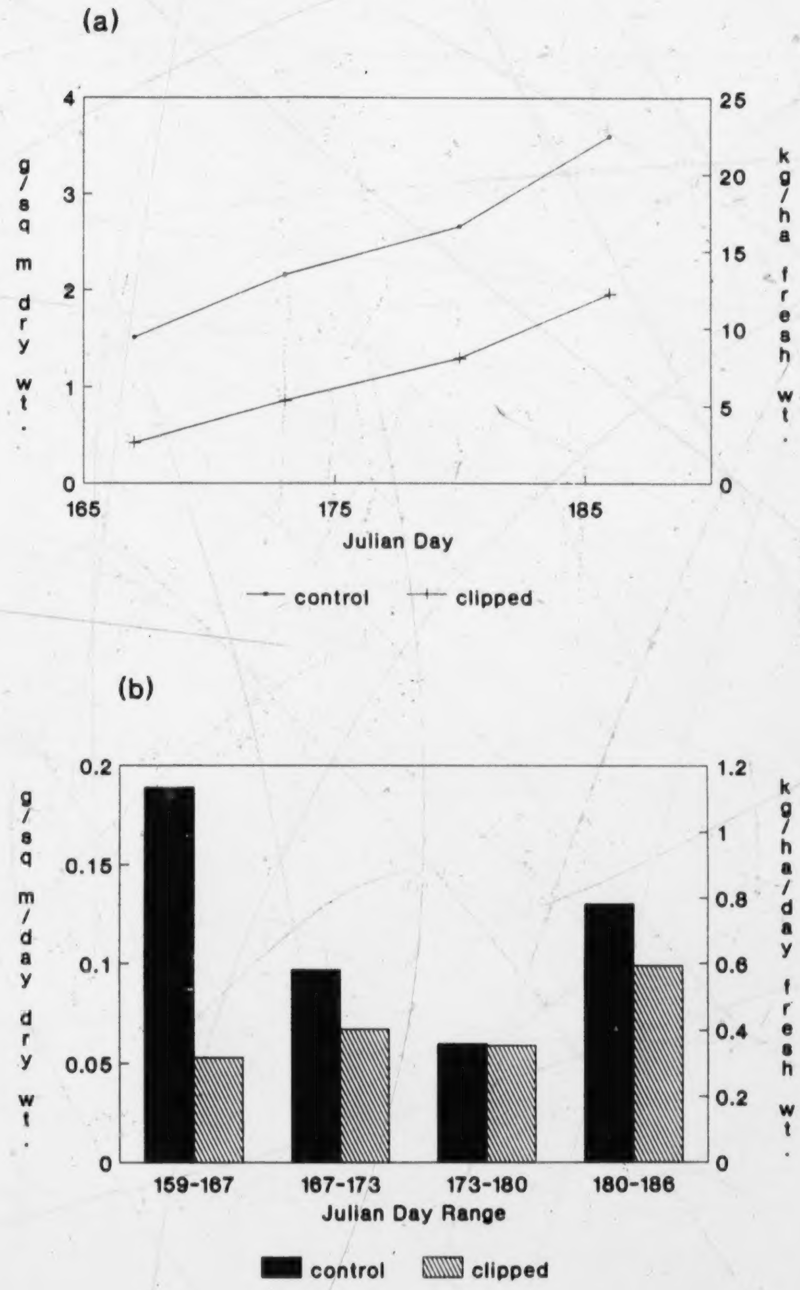


Figure 6.3 (a) Production of L. ochroleucus in the control and clipped treatments subsequent to clipping. (b) Production rate (PR) of L. ochroleucus during the sampling intervals after clipping in the control and clipped treatments.

depends on the regenerative residues remaining. Results from a study by Ryle et al. (1989) on the continuous defoliation of *Trifolium repens* supports this conclusion. They found that growth rate was largely a function of the number of expanded leaves remaining on stolons after defoliation. In *L. ochroleucus*, the amount of leaf area remaining after clipping was more important than the amount removed. Interception of photosynthetically active radiation (PAR) is closely related to the available leaf area and rises as leaf area increases (Loomis and Williams, 1969; Rhodes, 1973). The recovery of the growth rate in defoliated plants is governed by increasing leaf area index and light interception (Brougham, 1956). Ultimately, regrowth depends on the recovery of photosynthesis, a process which is facilitated by the marked allocation of dry matter to new leaf growth after defoliation (Culvenor et al., 1989b). Larger leaf area increases interception of solar radiation which in turn increases dry matter production (Watson, 1952; Donald and Black, 1958; Jameson, 1963; Shibles and Weber, 1966; Bjorkman, 1981). Since all plants were clipped to the same height they all had approximately the same leaf area and the same potential for PAR interception and production. Therefore, the pre-clipping height had no effect on the rate of regrowth.

After clipping, the proportion of *L. ochroleucus* plants growing was significantly lower than the proportion of control plants growing. This was especially true during the first week after clipping. Results reported by Culvenor et al. (1989) support this trend. They reported that a phase existed immediately after defoliation in which branches of subterranean clover did not grow and that the duration of this phase increased with severity of defoliation.

The amount of regrowth subsequent to clipping depends on the plant's carbohydrate reserves prior to clipping (Ehara and Macda, 1961; Ward and Blaser, 1961). After defoliation, there is a reallocation of carbon away from roots and branches, with a portion allocated to new leaf growth in grasses (Marshall and Sager, 1965; Ryle and Powell, 1975; Cladwell et al., 1981) and legumes (Fissel and Carlson, 1969; Hodgkinson, 1969; Pearce, 1969; Smith and Silva, 1969; Hoshino, Oizuma, and Okuba, 1972; Ryle, Powell and Gordon, 1985a; Culvenor et al., 1989a). The reserves needed for regrowth have to be relatively large because carbohydrate decline subsequent to clipping may be due primarily to root and stubble respiration (May and Davidson, 1958; May, 1960; Davidson and Milthorpe, 1965, 1966; Carlson, 1966). Morgan, Sprague and Sullivan (1953) after studying the carbohydrate balance of *Trifolium repens*, concluded that only carbohydrates above a certain minimum level were effective as reserve substances for regrowth. In addition to carbohydrate reallocation, nitrogen compounds may be mobilized to meet the energy requirements as the severity of defoliation increases (May, 1960; Davidson and Milthorpe, 1966; Culvenor et al., 1989a). The *L. ochroleucus* plants that did not grow subsequent to clipping may have had carbohydrate reserves too low to support maintenance respiration as well as regrowth. The *L. ochroleucus* plants that did grow had a large enough store of energy to buffer the reduced contribution from photosynthesis due to losses of photosynthetic tissue and thus could support maintenance respiration as well as regrowth.

Since the apical meristem of the *L. ochroleucus* plants was removed by the clipping treatment, any regrowth occurred from secondary meristems. The number, location and activity of meristems are particularly important limiting factors for re-establishment of foliage (Richards, 1984). The apical meristem is thought to suppress the growth of lateral buds by the production of auxins (Leopold, 1955; Gregory and Veale, 1957; Snnott, 1960; Jameson, 1963, 1964; Salisbury and Ross, 1985; Crawley, 1986). Removal of the terminal meristem releases lower buds which may then grow into replacement shoots (Leopold, 1955; Gregory and Veale, 1957; Snnott, 1960; Jameson, 1963, 1964; Salisbury and Ross, 1985; Crawley, 1986). Even if the clipped plants had reserves large enough to support maintenance respiration and regrowth but did not have the functional meristems required for regrowth they, would not grow.

The *L. ochroleucus* plants that did grow after clipping had higher growth rates than the control plants. This may be due to the mobilization of carbohydrates and/or nitrogen compounds from storage for shoot regrowth in cooperation with physiological adaptations to partial defoliation. The clipped plants may have been utilizing larger quantities of energy for growth coming largely from storage reserves while the control plants were relying on lesser amounts from current photosynthesis. May (1969) indicated, however, that additional carbohydrates above a minimum level did not result in additional growth once the basic requirements had been met. Conversely, Morgan, Sprague and Sullivan (1953) studied the carbohydrate balance of *Trifolium repens* and concluded that only carbohydrates above a certain minimum level were effective as reserve substances for regrowth. Trlica (1977) concluded from a review of the relevant literature, that the rate of regrowth was slower and the amount of regrowth was less for plants with lower carbohydrate levels. Richards (1984), referring to grasses, contended that this was the traditional concept whereby below-ground stored reserves were mobilized for use in shoot regrowth, but that current photosynthates were more important in foliage regrowth.

The photosynthetic capacity of plants has been shown to increase following defoliation because of increased stomatal and/or mesophyll conductance of CO_2 (Meidner, 1970; Hodgkinson et al., 1972; Gifford and Marshall, 1973; Hodgkinson, 1974; Painter and Detling, 1981). As well, there is a reduction in respiratory output from the plant parts remaining after partial defoliation (Davidson and Milthorpe, 1966; Ryle, Powell and Gordon, 1985; Culvenor et al., 1989b). If the combined effect of increased photosynthetic capacity and reduced respiratory output of the tissue remaining after the clipping of *L. ochroleucus*, occurred, then it would assist in providing the positive energy balance required for rapid regrowth. These physiological adjustments to partial defoliation subsequent to the clipping treatment may assist in explaining why the clipped plants that did grow had higher growth rates than the control plants.

Subsequent to clipping, the higher growth rates of the clipped plants were not large enough to make up for the reduced proportion of clipped plants growing relative to the control. This is illustrated by comparing the AGR between treatments. With higher AGRs the control plants exhibited higher production rates and biomass yields than the clipped plants during the early summer of 1989 in the aspen-dominated forest at MWRS.

The reduced production rate in clipped *L. ochroleucus* plants compared to control plants may not be altogether deleterious because the clipped plants may have a higher protein content. Cutting generally results in a higher per cent of protein in the forage (Brockingtin, 1960; Parsons and Davis, 1960; Jameson, 1963) and some research indicates that this increase was more than enough to offset yield losses (Folkins, Greenshields, and Nowosad, 1961). Jacobs (1952) and Colville and Torrie (1962) reported that dry matter yield and nitrogen per cent are inversely related. As clipping severity increases so does the likelihood that the plants will mobilize nitrogen compounds to meet the energy requirements for respiration and/or growth (May, 1960; Davidson and Milthorpe, 1966; Kigel, 1980; Culvenor et al., 1989). This is dependent on the availability of carbohydrates (Kigel, 1980). There most likely is a level of grazing intensity for *L. ochroleucus* where the increase in nitrogen offsets the decrease in dry matter production to maximize protein yield.

6.5 Conclusions

The severity of clipping, as represented by the plant size prior to clipping at a height of 25cm, did not influence the rate of regrowth.

This was due to the greater importance of leaf area remaining after clipping compared to the amount removed. Since all plants were clipped to the same height they all had approximately the same leaf area and the same potential for PAR interception and production.

The greater proportion of clipped plants that did not grow after clipping, relative to that of the control may be attributed to the clipped plants not having enough carbohydrate reserve for both respiration and regrowth. Clipping reduced leaf area and current photosynthesis which adversely effected carbohydrate production levels. Thus, plants that had reserve levels too low to support maintenance respiration as well as regrowth, did not grow during the four weeks subsequent to clipping. Even if the plants had reserves large enough to support respiration and regrowth, but did not have the functional meristems required to utilize these resources for regrowth, they would not grow.

The clipped plants that did grow after clipping had higher growth rates than the control plants. This may be due to the greater amount of resources put into tissue production by the clipped plants in conjunction with increases in their photosynthetic capacity and a reduction in their respiration rates. In a natural situation where ungulates did the clipping, the growth rate may be higher due to growth stimulation by ungulate saliva. Growth stimulations of up to 50% above control levels have been obtained by applying ungulate saliva or one of its constituents to manually clipped leaves (Reardon et al., 1972, 1974).

Even though the clipped plants that grew subsequent to clipping had higher growth rates than the control plants, clipping reduced production because a significantly smaller proportion of the clipped plants exhibited height growth compared to the control. Clipping of *L. ochroleucus* plants to a height of 25cm at the beginning of their reproductive/storage phase in aspen-dominated forests at MWRS resulted in a reduction in production compared to the un-clipped control plants. Whether this reduction in yield was associated with an increase in protein content requires further investigation.

Grazing intensities that remove less than 50% of the tissue of *L. ochroleucus* may be less detrimental to production by increasing the proportion of plants growing and possibly increasing growth rate. As well, there is evidence that root growth and nutrient uptake are inhibited by defoliation intensities where more than 40-50% of the tissue is removed (Jameson, 1963). Less severe clipping would provide more leaf area for photosynthate production and increase the number of auxiliary buds. With an increase in the number of axillary buds the probability of there being a functional one would increase, especially if they lose function with age.

On a population level, less intense grazing may also increase production because of increases in the number of ramets. Less intense grazing would be less taxing on energy reserves. Higher positive energy balances increase ramet production capabilities (Harper, 1977). Weatherill and Keith (1969) found that *L. ochroleucus* per cent frequency increased under light cattle grazing intensity.

To determine the best time during the growing season for the utilization of *L. ochroleucus* requires more research. Plants are affected more by defoliation at certain phenological stages and it is desirable to know at what stages forage species can be utilized without severe carbohydrate depletion (Trlica, 1977). A better knowledge of the seasonal carbohydrate cycle of *L. ochroleucus* is required to maximize its production by optimizing the timing of its utilization. Since *L. ochroleucus* is most commonly utilized by ungulates during the spring and early summer (Blood, 1966; Weatherill and Keith, 1969), this research provides results on the response of *L. ochroleucus* to clipping under conditions similar to the natural grazing regime.

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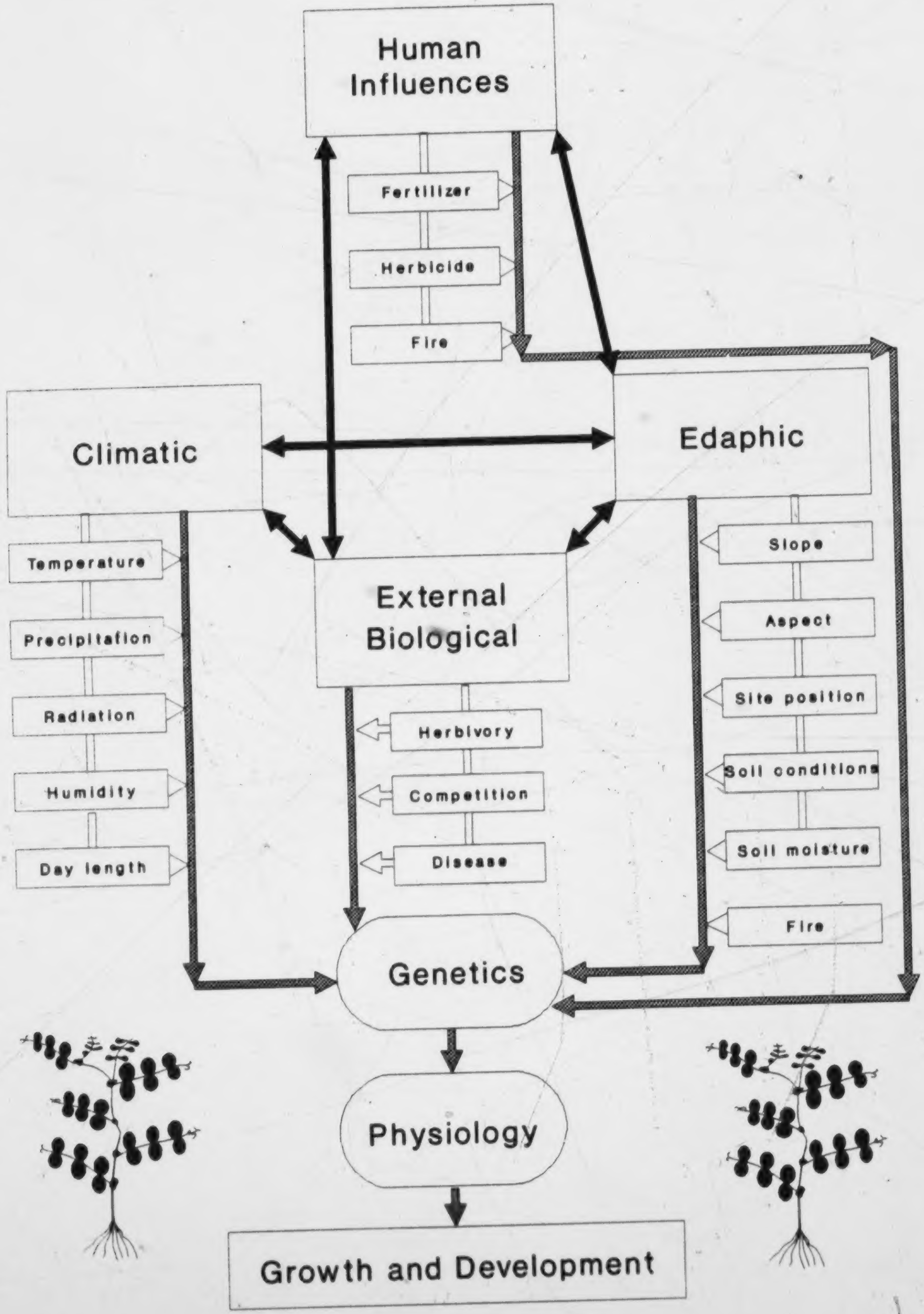
7.0 General Overview

Lathyrus ochroleucus Hook. is an important forage species for wapiti, deer, and cattle. It is preferentially selected (Blood, 1966; Weatherill and Keith, 1969; Kufeld, 1973; Hunt, 1979; Watson et al, 1980; Smoliak et al, 1988; Adams et al, 1986) and utilized much in excess of its availability relative to other forbs (Weatherill and Keith, 1969). Proper rangeland management requires detailed knowledge of the ecosystem, including the plant species important in herbivore diets. *L. ochroleucus* is an important species of the aspen and balsam poplar-dominated forests of western Canada. More than 30% of the area of the prairie provinces has forest regions (as described by Rowe, 1972) structurally dominated by *Populus* species (Telfer and Scotter, 1975). These forest areas are considered marginally-arable. However, they are important habitat for ungulates and their use for cattle and game ranching is increasing (Ad hoc Committee, 1976). With increased resource development such as agricultural expansion, oil exploration, and forestry and mining activities it is of vital importance to properly manage this limited rangeland resource. Since the welfare of the individual plant is the foundation of the range, a knowledge of the function of the individual plant species in response to the environment in which it lives is an essential prerequisite to the proper management of our rangeland resources (Tueller, 1977; Sosebee, 1977).

The growth and development of *L. ochroleucus* is ultimately genetically controlled, however, the genetics and physiology of the species were not the focus of this study. The individual plant (genet) is affected by climatic, edaphic, human, and external biological attributes which together induce physiological responses that are externally expressed as growth and development (Figure 7.1). Within spatial and temporal limitations, the interaction and interdependency of these factors varies. As well, in time and space the degree of

Figure 7.1 The growth and development of *L. ochroleucus* is a direct result of physiological processes, which, in turn, are governed by the interaction of the genetic makeup of the plant and it's environment. The genetic makeup of the individual plant is acted upon by climatic, edaphic, human, and external biological attributes which together induce physiological responses that are externally expressed as growth and development. The large square boxes represent environmental controls, with the affiliated small square boxes representing some of the factors that are within the category. The solid black arrows illustrate the interaction and direction of influence of the environmental factors. All of the environmental factors either directly or indirectly affect the growth and development of the plant (shaded arrows).


Human Influences
Fertilizer
Herbicide
Fire
Climatic
Edaphic
Temperature
Precipitation
Radiation
Humidity
Day length
External Biological
Herbivory
Competition
Disease
Slope
Aspect
Site position
Soil conditions
Soil moisture
Fire
Genetics
Physiology
Growth and Development

influence of climatic, edaphic, external biological, and human intervention on the growth and development of *L. ochroleucus* varies.

7.1 Growth and Development

The seasonal growth of *L. ochroleucus* can be represented with the use of a second degree polynomial equation (Figure 4.4). This growth model had two distinct phases: the linear and the reproductive/storage. These are reflective of the changing physiological functions of the plant and the partitioning of resources to meet these specific needs. The linear phase was dominated by vegetative growth while the reproductive/storage phase was dominated by reproductive growth and assimilate storage. *L. ochroleucus* puts energy reserves, stored from the previous season, into vegetative growth early in the growing season. Underground storage organs such as rhizomes and roots may contain as much as 60% carbohydrate at the end of the growing season (Mooney, 1972). This carbohydrate accumulation provides reserves for new vegetative growth in the early spring resulting in a significant depletion of these reserves (Trlica, 1977). These new shoot systems produce assimilates that are used by the plant for further vegetative growth or are stored and later utilized when net photosynthesis can not meet the plant's demands (Trlica, 1977; Rechcigl, 1982; Larcher, 1983). Once the accumulated food supply is adequate the plant is ready to flower and reproductive structures take precedence over the storage process (Daubenmire, 1974; Trlica, 1977; Rechcigl, 1982; Larcher, 1983; Nobel, 1983). Near the end of the growing season, the accumulated assimilates move preferentially to the belowground parts of the plants where they are stored until the following season (Larcher, 1983; Nobel, 1983). Several *L. ochroleucus* plants (ramets) can be interconnected through an elaborate system of rhizomes. This colonal growth pattern means that a group of ramets (collectively called genets) are genetically identical and to some degree interdependent on resources

(Kays and Harper, 1974). At every stage in the growth and development of the plants the resources can potentially move among the ramets as long as these links (rhizomes) have not been severed (Harper, 1977). There is no question that the partitioning of resources among shoots affects their growth and development, however, this was not the focus of this study. The growth and development of *L. ochroleucus* plants follow the pattern described above, with the rate of growth and timing of development determined through the interaction of the plants genetic makeup with environmental variables (climate, edaphic, external biological, and human influences) (Figure 7.1).

An important result of growth and development in a range management context is the amount of forage produced. The production of 25.6 kg ha^{-1} fresh matter for *L.ochroleucus* in the aspen-dominated forest at MWRS during the spring and early summer of 1989 (Figure 5.11a) suggests it could contribute significantly to the forage resource. This is especially true due to its high forage quality (Adams et al, 1986). The quantity of *L. ochroleucus* available for forage in aspen-dominated forests during the spring and early summer can be predicted (Chapter 5).

7.2 Edaphic Influences

Influences that are edaphic in nature definitely affect the growth and development of *L. ochroleucus*. Edaphic factors influence and are influenced by biological and climatic conditions as well as human intervention (Figure 7.1). Since the growth of *L. ochroleucus* plants were monitored at only three sites, the statistical evaluation of the effect that seasonally static edaphic variables (such as slope, aspect, and site position) had on growth, was not possible. Although the effect of these variables on the growth of *L. ochroleucus* was not directly evaluated they manifested their effects through site differences in microclimate.

Due to the similarity of the study sites with respect to their soil characteristics (Table 5.1), and the small number of sample sites (three), the influence that a site's soil characteristics had on the growth of *L. ochroleucus* was not investigated. All three study sites occurred on Orthic Grey Luvisol soils of the Cooking Lake soil series. However, due to the temporal variability in soil moisture content, enough data were collected to evaluate its effects on the growth of *L. ochroleucus*.

Soil moisture content is the result of the interaction of climatic and soil conditions (Figure 7.1). Soil moisture was treated as an edaphic factor since within the Cooking lake moraine area, the spacial distribution of soil moisture is dominantly influenced by topography and soil texture (Figure 7.1). Soil moisture content during the spring and early summer (6 May to 8 June) of 1989 at MWRS was not a factor limiting the growth of *L. ochroleucus*. It was expected that soil moisture would not limit the growth rate of *L. ochroleucus* during its linear growth phase in a "normal" year in aspen-dominated forests. This is due to the extreme rarity of soil moisture deficits at this time of year in this region.

7.3 External Biological Influences

Biological factors external to the plant, yet influential in its growth and development include herbivory, disease, and competition (Figure 7.1). The effect of disease on the growth and development of *L. ochroleucus* was not investigated. Competition or interference from another part of the same genet, from a different genet of the same species or members of different species could affect the rate of growth and development of *L. ochroleucus*. This may occur through the depletion of limited resources but only when the depletion zone of one plant includes the zone available to another (Harper, 1977). Differences in the growth of *L. ochroleucus* among sites caused by differences in the competition between *L. ochroleucus* and its neighbours was not found.

This was due to the similarity of the study sites with respect to their species composition and cover/distribution characteristics (Figure 3.2).

At the individual level, competition between *L. ochroleucus* plants and their neighbours for the light resource was not dominant in affecting their growth. A plant that is slightly taller may receive considerably more radiation due to its superior position above competitors in the herbaceous canopy layer. Within closed-canopied herbaceous vegetation, small differences in plant height are associated with large changes in the intensity, direction, and quality of radiation they receive (Grime, 1979). Plant height was not a dominant factor governing the growth of *L. ochroleucus* except early in the growing season (Figure 4.5). Early in the growing season, the herbaceous canopy had not fully expanded, thus, the greater shading of shorter plants which would have given the larger plants a competitive advantage, did nor occur. The larger plants had higher growth rates because they had greater leaf area. As leaf area increases so does the interception of PAR, which, in turn causes assimilation to increase. The larger plants would therefore accumulate more carbohydrates and exhibit higher growth rates than the smaller plants.

Although "herbivory" may include anything from insects to large ungulates the later were of concern in this study. Herbivory usually involves removal of only a portion of a plant, leaving the remainder to regenerate. In general, the more frequent and severe the grazing (clipping) the more dry matter yield is depressed. Davidson and Donald (1958) suggested that the amount of tissue (leaf area) remaining after grazing may be more important than the amount removed (From Jameson, 1963). Harper (1977) indicates that damage to the apical meristems may have effects far greater than the fraction of the plant body that is eaten. He also states that when a plant loses tissue the loss of mineral nutrients may be more important than the loss of energy involved.

The height of *L. ochroleucus* plants before clipping at a height of 25 cm, did not influence their rate of regrowth. The pre-clipping height of L. ochroleucus represents the severity of the clipping treatment since all plants were clipped to the same height. Thus, subsequent to clipping, all plants had approximately the same leaf area and the same potential for PAR interception and production. Results from a study by Ryle et al (1989) on the continuous defoliation of white clover support this conclusion. They found that growth rate was largely a function of the number of expanded leaves remaining on stolons after defoliation. By clipping *L. ochroleucus* plants at different heights, the influence that the quantity of tissue remaining after clipping has on growth rate, could be determined.

The greater proportion of clipped *L. ochroleucus* plants that did not grow after clipping, relative to that of the control (Figure 6.1a), may be attributed to the clipped plants requiring a relatively large level of carbohydrate reserve for respiration and regrowth due to the reduction in current photosynthetic production caused by low leaf area. Thus, the plants that had reserve levels too low to support maintenance respiration as well as regrowth, did not grow during the four weeks after the clipping treatment. Even if the plants had reserves large enough to support respiration and regrowth, but did not have the functional meristems required to utilize these resources for regrowth, they would not grow.

The clipped plants that did grow after clipping had higher growth rates than the control plants (Figure 6.1b). This may be due to the greater amounts of resources put into tissue production by the clipped plants in conjunction with increases in their photosynthetic capacity and a reduction in their respiration rates. In a natural situation where ungulates did the clipping, the growth rate may be higher due to growth stimulation by ungulate saliva. Growth stimulations of up to 50% above control levels have been obtained by applying ungulate saliva or one of its constituents to manually clipped leaves (Reardon et al, 1972, 1974).

Even though the clipped plants that grew subsequent to clipping had higher growth rates than the control plants, clipping reduced production because a significantly smaller proportion of the clipped plants exhibited growth compared to the control (Figure 6.3). Clipping 5 of *L. ochroleucus* plants to a height of 25cm at the beginning of their reproductive/storage phase in aspen-dominated forests at MWRS resulted in a reduction in production compared to the un-clipped control plants. Whether this reduction in yield is associated with an increase in protein content requires investigation.

Grazing intensities that remove less than 50% of the tissue of *L. ochroleucus* may be less detrimental to production by increasing the proportion of plants growing and possibly increasing growth rate. As well, there is evidence that root growth and nutrient uptake are inhibited by defoliation intensities where more than 40-50% of the tissue is removed (Jameson, 1963). Less severe clipping would provide more leaf area for photosynthate production and increase the number of axillary buds. With an increase in the number of axillary buds the probability of there being a functional one would increase, especially if they lose function with age.

On a population level, less intense grazing may also increase production because of increases in the number of ramets. Less intense grazing would be less taxing on energy reserves. Higher positive energy balances increase ramet production capabilities (Harper, 1977). Weatherill and Keith (1969) found that *L. ochroleucus* per cent frequency increased under light cattle grazing intensity.

To determine the best time during the growing season for the utilization of *L. ochroleucus* requires more research. Plants are affected more by defoliation at certain phenological stages and it is desirable to know at what stages forage species can be utilized without severe carbohydrate depletion (Trlica, 1977). A better knowledge of the seasonal carbohydrate cycle of *L. ochroleucus* is required to maximize its production by optimizing the timing of its utilization. The best time to utilize *L. ochroleucus* would be during a temporal window which begins long enough after spring leaf flush and flowering to allow carbohydrate levels to rebound. Grazing would have to cease, leaving *L. ochroleucus* enough time before senescence so to replenished and store carbohydrates for spring leaf flush the next season.

7.4 Climatic Influences

Climate is the statistical attributes of the weather over any specified region for a specified interval of time. The interaction of atmospheric phenomena with local biological and edaphic conditions and human influences, together over space and time determine the climate of an area (Figure 7.1). Similarly the edaphic, and external biological conditions and human influences in an area are influenced by its climate (Figure 7.1) The 1989 growing season was the time interval in which the influence of climate on the growth and development of *L. ochroleucus* was studied. Based on the variability in the growth of *L. ochroleucus* in the three sampling sites at MWRS, spatially it is apparent that mesoclimate had a stronger influence on its growth than microclimate (Figure 5.3). The mesoclimatic influences of the regional weather patterns were approximately 21 times stronger in their influence on *L. ochroleucus* growth than the microclimatic differences among sample sites. This suggests that official meteorological records which reflect mesoscale climate may be usefully applied in evaluating *L. ochroleucus* growth. Lindsey and Newman (1956) after a statistical analysis using official temperature data to evaluate the relationship between phenology and temperature concluded:

> ... a sufficiently close parallelism exists between the official meteorological records and temperatures actually influencing the plant for such records to be ecologically useful when interpreted by a suitable method.

Although many climatic variables are important in their influence on the growth *L. ochroleucus*, temperature was the variable of focus in this study. The effects of precipitation on the growth of *L. ochroleucus* were not dealt with directly, but were considered through their influence on soil moisture content. In addition, the influence of radiation, humidity and day length were not evaluated, however, they affect the temperature regime (Figure 7.1).

The increase of *L. ochroleucus* growth rate with average mean daily temperature had a Q_{10} of 2.56 which indicates that its growth rate is a chemically controlled process. Processes with Q_{10}'s of 1.3 to 1.5 are physically controlled processes (i.e. gas or water diffusion) where as most biochemical and chemical reactions have Q_{10}'s near two (Noble, 1983). The linear growth response of *L. ochroleucus* to increasing temperatures up to the "optimal" (Figure 5.6, 5.7) may be explained by the effects of temperature on the rates of chemical reactions and the increased tendency of plants to store larger quantities of sugars and carbohydrates at lower temperatures. The quantity of energy reserves a plant has will influence it's response to high temperatures. The energy consumptive processes of maintenance respiration and photorespiration increase faster with temperature than photosynthesis. Thus, at high temperatures energy is used at a faster rate than it is produced. *L. ochroleucus* plants that had energy reserves too low to buffer this increased energy loss, ceased to grow. The growth rates of the plants that did grow, however, responded to average daily maximum and mean temperatures in an almost linear fashion (Figure 5.7 a, c), possibly due to them having large enough energy reserves to buffer the effects of increased respiration at the higher temperatures. The growth rate of the plants that exhibited a linear growth response to average daily maximum and mean temperatures was reduced at the higher average minimum daily air temperatures encountered during the study. The increased energy reserve utilization caused by increased maintenance respiration at higher night temperatures (higher minimum air temperatures) reduces growth rates by reducing the quantity of reserve available for growth.

The vegetative growth of *L. ochroleucus* is affected by the temperature regime of both its shoots and roots. The separation of these effects and the determination of its lethal, threshold, and optimum temperature ranges requires controlled environmental experimentation. The temperature regime of this study and its effects on *L. ochroleucus* growth, however, can be considered representative of their relationship in aspen-dominated forests.

7.5 Human Influences

The affects of human intervention in natural systems can be seen all around us. This is one reason that proper management of our resources for sustainable yield and prevention of resource deterioration is of preeminent importance. When considering native rangelands where *L. ochroleucus* plants are found, if human intervention goes beyond the stocking of animals, it usually involves clearing, breaking, and seeding of those areas with agronomic species. This causes large changes in local climatic, edaphic and biological conditions as well as the eradication of the *L. ochroleucus* plants that were present. Less severe human influences which leave tissue to regrow or regenerate include fertilization, herbicide application, and burning (Figure 7.1). Occasionally, however, prescribed burns and herbicide treatments are used to control woody vegetation in forest clearing and in the understory of aspen forests. A reduction in the abundance of *L. ochroleucus* after percribed burns (Anderson and Bailey, 1980) and the application of herbicide (Hilton and Bailey, 1974) has been found in the Aspen Parkland of Alberta. Research into the use of herbicides and fire in aspen-dominated forests as well as stocking rates, and rotational grazing may provide some of the required information to better manage this limited forage resource.

7.6 Summary Statement

This research reveals more questions than it answers. The right questions, however, must be asked before they can be answered. This study takes the first step in the acquisition of knowledge about the autecology of *L. ochroleucus*. *L. ochroleucus* is, however, only one of many native forage species of Canada's northern forests whose autecology is little understood. The more we can learn about the function of the individual plant species which compose this vital but limited rangeland resource the better we can prevent its deterioration through effective management.

7.7 References

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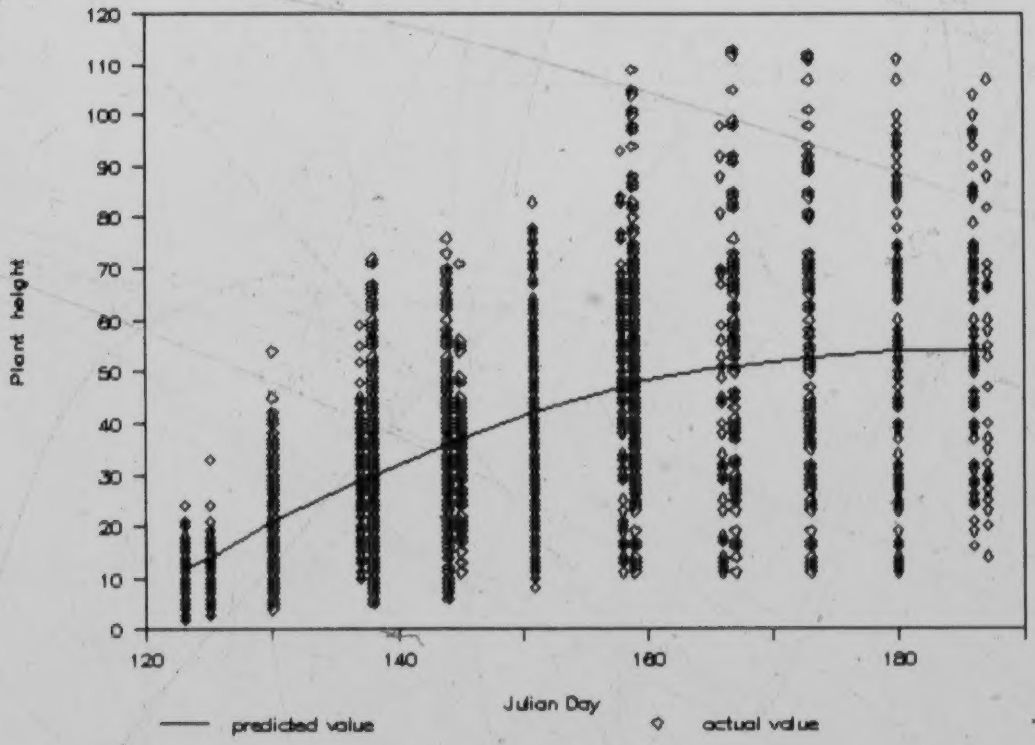
APPENDIX I
Soil and Site Characteristics

Attribute/Site	P1	P2	P3
aspect	ESE	WNW	E
slope(%)	0-5	5-10	15-25
site position	apex	middle	middle
parent material	till	till	till
LFH			
depth (cm)	6-0	5-0	6-0
moist color	black	black	black
pH	7.4-7.8	7.4-7.8	7.4-7.8
Ahe			
depth (cm)	0-3	0-4	0-4
moist color	10YR 3/2	10YR 3/2	10YR 3/2
texture	SiCL	SiCL	SiCL
pH	6.6-7.3	7.4-7.8	6.1-6.5
Ae			
depth (cm)	3-10	4-12	4-13
moist color	10YR 5/3	10YR 5/4	10YR 4/2
texture	SiCL	SiCL	SiCL
pH	5.6-6.0	6.1-6.5	6.1-6.5
Bt			
depth (cm)	10-70	12-85	13-80
moist color	10YR 3/4	10YR 5/4	10YR 4/4
texture	SiC	SiC	SiC
pH	6.1-6.5	6.1-6.5	6.1-6.5
BC			
depth (cm)	70-105	85-95	80-100
moist color	10YR 4/3	10YR 5/4	10YR 4/3
texture	SiCL	SiCL	SiCL
pH	6.1-6.5	6.1-6.5	6.1-6.5
CK			
depth (cm)	105+	95+	100+
moist color	10YR 5/3	10YR 5/3	10YR 5/3
texture	SiCL	SiCL	SiCL
pH	7.4-7.8	7.4-7.8	7.4-7.8

APPENDIX II

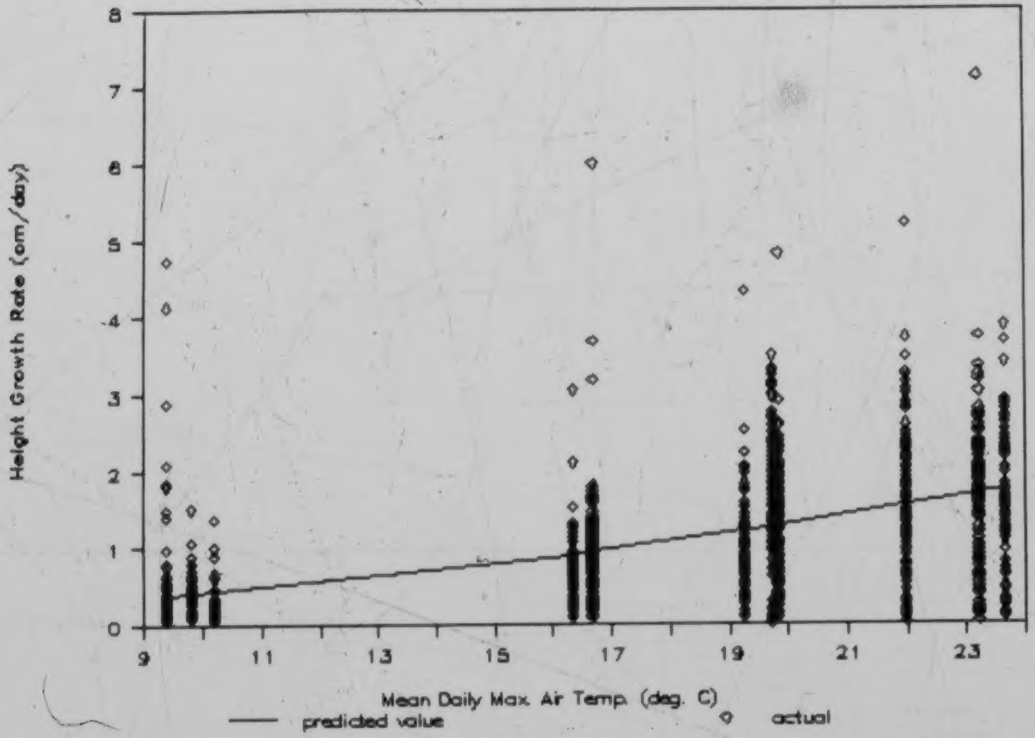
SUPPLEMENTARY DATA FOR HEIGHT GROWTH RATE MODELS

Figure 4.4 Supplementary Data



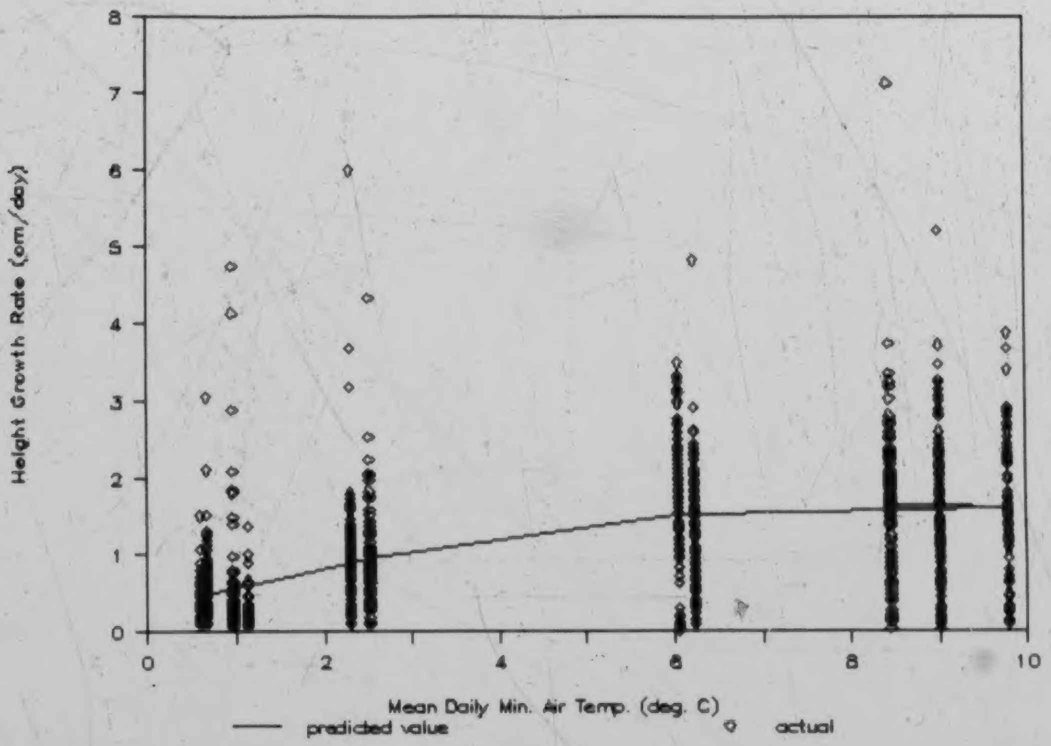
```
                       Analysis of Variance

                    Sum of           Mean
Source      DF     Squares         Square    F Value     Prob>F

Model        2 359347.76276 179673.88138     659.428     0.0001
Error     2189 596435.12019    272.46922
C Total   2191 955782.88295

    Root MSE      16.50664     R-square        0.3760
    Dep Mean      36.99649     Adj R-sq        0.3754
    C.V.          44.61678

                       Parameter Estimates

                 Parameter      Standard    T for H0:
Variable  DF      Estimate         Error   Parameter=0   Prob > |T|

INTERCEP   1   -343.961965   25.45843927       -13.511       0.0001
DATE       1      4.358572    0.33566989        12.985       0.0001
DATESQ     1     -0.011928    0.00109564       -10.886       0.0001
```

Figure 5.7a Supplementary Data



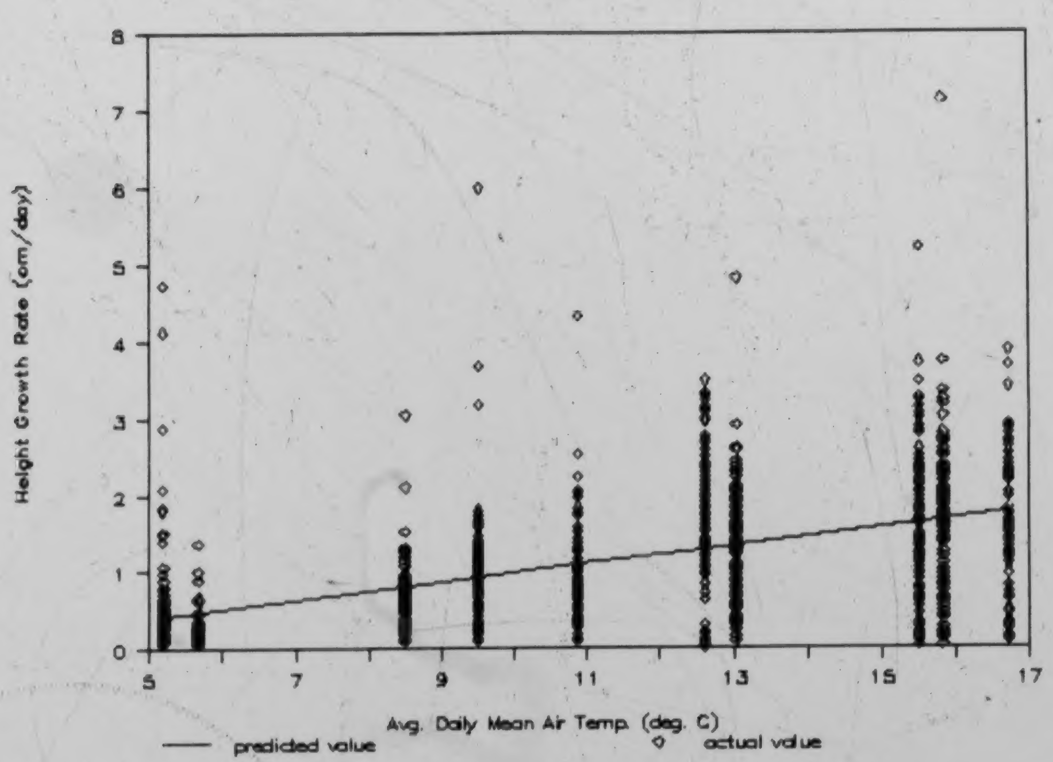
```
                    General Linear Models Procedure

                        Sum of             Mean
Source          DF     Squares            Square       F Value     Prob>F


Model            2   185.3046734       92.6523367     144.47       0.0001
Error          893   572.7184623        0.6413421
C Total        895   758.0231357

     R-Square          C.V.            Root MSE       GR Mean

     0.244458       71.12354          0.800838      1.12598214

                          Parameter Estimates

                    Parameter       T for H0:      Prob          Stanard
Variable            Estimate      Parameter=0     > |T|         Error

INTERCEP          0.1399253902        0.41        0.6846      0.34441163
MAXA              0.0004523325        0.01        0.9920      0.04512369
MAXASQ            0.0028739476        2.09        0.0372      0.0013774
```

Figure 5.7b Supplementary Data



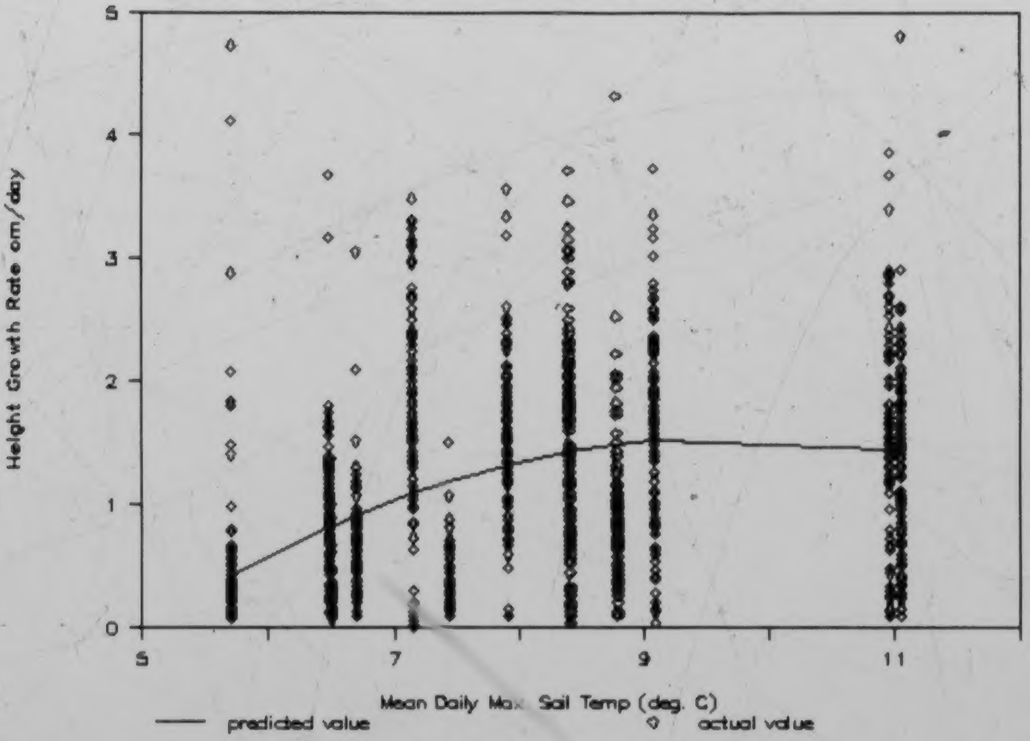
```
                    General Linear Models Procedure

                       Sum of          Mean
Source          DF     Squares         Square       F Value     Prob>F

Model            2   198.5910252    99.2955126      158.50      0.0001
Error          893   559.4321106     0.6264637
C Total        895   758.0231357

      R-Square          C.V.           Root MSE         GR Mean

      0.261985        70.29371         0.791495        1.12598214

                          Parameter Estimates

                    Parameter       T for H0:     Prob        Stanard
Variable             Estimate      Parameter=0    > |T|       Error


INTERCEPT          0.2811666802        4.22       0.0001     0.06660237
MINA               0.3080218324        7.96       0.0001     0.03870941
MINASQ             -.0175719282       -4.62       0.0001     0.00380064
```

Figure 5.7c Supplementary Data



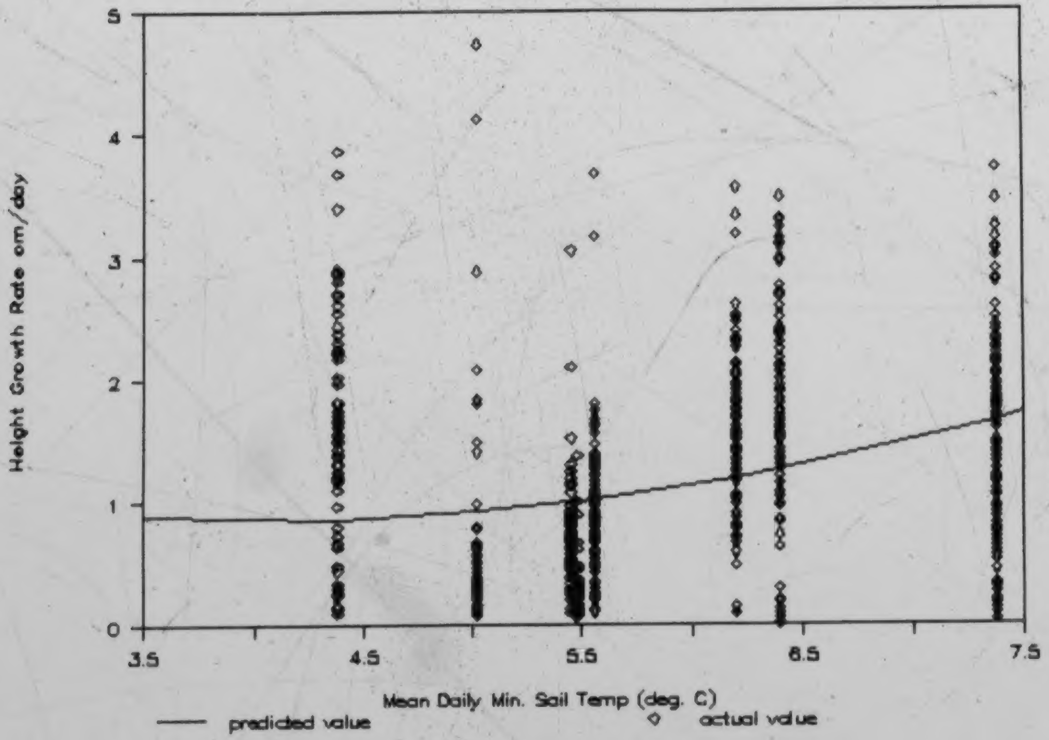
```
                    General Linear Models Procedure

                         Sum of          Mean
Source          DF      Squares         Square       F Value     Prob>F

Model            1    194.3993328   194.3993328      308.35      0.0001
Error          894    563.6238029     0.6304517
C Total        895    758.0231357

      R-Square         C.V.            Root MSE         GR Mean

      0.256456      70.51709          0.794010       1.12598214

                              Parameter Estimates

                      Parameter       T for H0:      Prob        Stanard
Variable              Estimate       Parameter=0    > |T|        Error

INTERCEPT          -.1871580201        -2.36        0.0186      0.07934598
MEANA              0.1172320408        17.56        0.0001      0.00667613
```

Figure 5.9a Supplementary Data



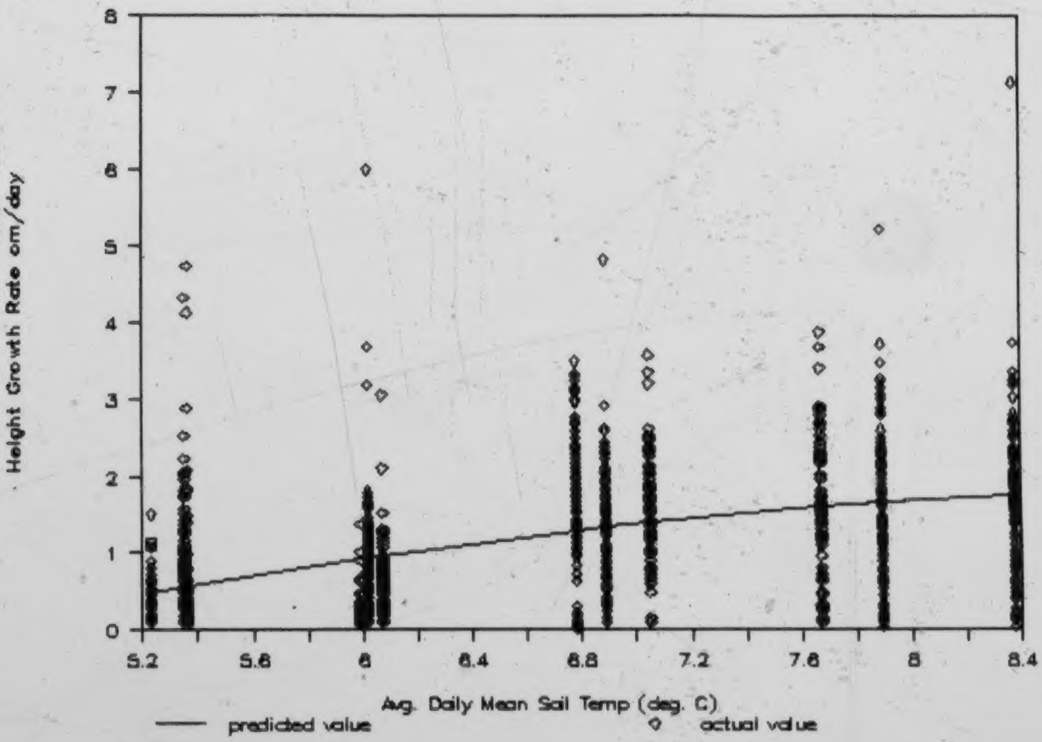
```
                          Analysis of Variance

                          Sum of         Mean
     Source        DF        Squares       Square      F Value     Prob>F

     Model          2      107.48824     53.74412       74.651     0.0001
     Error        986      709.86397      0.71994
     C Total      988      817.35221

     Root MSE         0.84849       R-square        0.1315
     Dep Mean         1.16709       Adj R-sq        0.1297
     C.V.            72.70186

                          Parameter Estimates

                   Parameter      Standard      T for H0:
   Variable  DF     Estimate         Error     Parameter=0   Prob > |T|

   INTERCEP   1    -4.964228    0.72588092          -6.839       0.0001
   MAXS       1     1.336512    0.17530074           7.624       0.0001
   MAXSSQ     1    -0.068570    0.01025568          -6.686       0.0001
```

Figure 5.9b Supplementary Data



```
                         Analysis of Variance

                           Sum of         Mean
Source       DF           Squares       Square     F Value      Prob>F

Model         2          85.43457     42.71729      57.546      0.0001
Error       986         731.91764      0.74231
C Total     988         817.35221

    Root MSE           0.86157     R-square        0.1045
    Dep Mean           1.16709     Adj R-sq        0.1027
    C.V.              73.82255

                         Parameter Estimates

                     Parameter     Standard    T for H0:
Variable     DF       Estimate        Error   Parameter=0    Prob > |T|

INTERCEP      1       1.885556   0.20210476         9.330        0.0001
MINS          1      -0.532801   0.08877800        -6.001        0.0001
MINSSQ        1       0.067934   0.00905958         7.499        0.0001
```

Figure 5.9c Supplementary Data



```
                    Analysis of Variance

                       Sum of         Mean
Source        DF      Squares       Square     F Value      Prob>F

Model          2    168.49798     84.24899     128.025      0.0001
Error        986    648.85424      0.65807
C Total      988    817.35221

    Root MSE         0.81121      R-square        0.2062
    Dep Mean         1.16709      Adj R-sq        0.2045
    C.V.            69.50748

                      Parameter Estimates

                Parameter    Standard      T for H0:
 Variable  DF    Estimate       Error     Parameter=0   Prob > |T|

INTERCEP    1 -4.817723    1.31735919      -3.657       0.0003
MEANS       1  1.395030    0.39595739       3.523       0.0004
MEANSSQ     1 -0.072890    0.02923515      -2.493       0.0128
```

APPENDIX III
HEIGHT DATA

L. ochroleucus height data collected at Ministik Wildlife Research Station in 1989. A value of 5000 represents a missing value.

Site P1

Plant No.	Julian Days 124	130	138	144	151	159	167	173	180	187
1	17.3	42.2	63.5	63.5	72.5	86.5	25	25	25	25
2	9	9	14.8	16.5	23.8	49	37.8	38	38.7	39
3	15.8	37.9	54.8	54.9	55	55	55	55	55	5000
4	5	27.5	29	34.9	35	35	25	25	25	25
5	8.8	27.4	41.3	42	46.7	53.2	25	25	25	25
6	5000	5000	5000	5000	5000	5000	5000	5000	5000	5000
7	16.1	32.5	54.5	56.8	67	80	25	26	25	25
8	11.7	29.1	41.3	45.3	44.8	51	25	25	25	5000
9	14.1	36.8	55.5	57.5	62.1	28.6	31.8	43.9	52.8	5000
10	5.9	24	45.4	47.3	52.1	68.3	25	25	63	69.6
11	6.6	28.6	35.3	36.5	38.1	38.8	25	25	25	5000
12	4	23	40.3	40.5	40.4	40.7	41.2	41	64.1	67
13	13.8	25.6	38.3	38	43.3	51.5	25	25	25	25
14	13.5	44.9	70.7	72.5	72.2	79.8	25	25	25	5000
15	9.7	37	63.2	66.5	78.1	104	111.6	111.2	111.3	5000
16	9.1	32.3	45.6	45.8	51	68.3	25	25	25	5000
17	6.4	14.4	25	26.4	32.5	43.3	25	33.8	45	95.7
18	6.4	26.8	41.5	43.8	49.7	65	71.2	71	71	71
19	6.8	26	31	31.4	31.4	33.8	25	25.4	36.3	36.5
20	9.4	18.8	19.3	19.4	19	19	37.9	40	39.9	5000
21	7.4	5000	7.5	8.7	30.8	56.6	82.3	92.4	95.7	95.5
22	2	26	27.5	27.9	28	28.5	25	25.5	37.4	11.3
23	13	23.2	17.9	19.3	31	49.6	28.6	35.9	45.1	51.4
24	6.4	32.9	51.2	52.8	59.3	59.6	25	25	25	25
25	21.1	34	40.8	41.2	47.5	70	81.4	87.9	94.7	140.4
26	20.4	28.4	28.6	28.5	40.6	59.1	65.7	62.3	5000	5000
27	14.9	28.7	28.3	28.2	29	47.3	113.4	112.3	5000	5000
28	14.8	36.1	51.7	55.1	62.6	68.5	25	25	25	25
29	9.2	24.3	38.2	40.5	45.4	52.7	25	25	25	25
30	10.2	27.9	28.1	28	28	46.5	28.1	52.4	78.4	78.5
31	7.9	31.9	53.2	57	68.2	73	79	25	25	5000
32	9.1	18.6	19.6	20	27.3	41.2	49.3	58.1	58.3	5000
33	11.5	35.9	59.5	63.2	70.7	82	85	90.2	89.7	90
34	13.5	16	18.4	18.3	24.6	39.2	5000	5000	5000	5000
35	8.5	15.5	15.7	16	19	35.5	25	25	25	25
36	5000	5000	5000	5000	5000	5000	5000	5000	5000	5000

37	13.4	42.2	62.2	62	74.5	97.5	25	25	25	5000
38	11.4	11	11.5	11.5	20.5	50.2	25	25	25	5000
39	7.5	40.3	66.8	5000	75.5	100	26.4	40.6	49.3	5000
40	9.8	14.6	14.5	16.4	18.7	33.5	25	25	25	47.7
41	15.1	15	15.5	24.4	29.9	41	41.4	41.4	42.3	5000
42	8.4	15.9	16.5	16.5	21.6	45.5	75.8	79.8	85.7	5000
43	5.1	5.7	16.6	17.2	23.2	47.5	25	5000	36.8	36.8
44	5.8	9.8	9.4	10	9.7	23.9	72.9	72.5	73.7	73.5
45	10.1	29.9	51.4	51.1	62	82.7	83.4	83.7	84	84
46	7.4	35.2	59	62	70.6	87.5	25	25	33	50.4
47	4.6	4.2	5	16	5000	5000	5000	5000	5000	5000
48	3.4	25.1	36.2	37.6	37.4	41	64.5	64.7	64.5	5000
49	8	22.3	37.9	40.7	42.9	59	25	25	25	25
50	11.3	19.1	29.8	30.1	33.4	43.1	25	25	25	5000
51	5000	5000	5000	5000	5000	5000	5000	5000	5000	5000
52	9.5	24.9	40	42.5	49.7	52.3	56.3	57	58	5000
53	11.3	24.8	42.6	45.6	53.8	66.5	25	25	25	5000
54	16.5	20.7	39.6	40	44	53.3	54.4	54.7	55.5	55
55	17.5	36.8	49.7	52.1	59.5	69.6	25	25	25	5000
56	11	37.3	62.5	64	70.7	71.3	25	25	25	25
57	10.5	23.5	6.9	9	18	45.7	62.8	67.5	68.2	69
58	14	32	52	52	61	81.7	25	25	25	25
59	7	20.1	30.7	30.5	32.4	36.6	36.9	36.5	36.9	43.7
60	11.9	25.2	44.3	45.5	51.2	73.4	84.1	84.8	84.8	84.8
61	8.1	32	57.2	68	68.2	69.7	25	25	25	25
62	12	25.4	25	25	27.1	44.1	25	25	25	5000
63		30.7	31.4	31.6	32	48.2	59.2	56.7	69.8	75
64	11	22	21.8	22.2	23.1	42.5	56.8	5000	5000	79.5
65	9.8	25.8	25.7	25.8	25.4	37.1	61.8	64.2	64	5000
66	7.6	21.6	29.8	30	30.9	32.6	41.4	45.3	45.2	45.2
67	9.3	37.4	65.2	70	75.4	105.1	25	25	25	25
68	13	31.2	43.2	55.6	62	67.1	25	25	25	25
69	6	22.1	38.6	40.6	46.1	66	68.1	68.1	68	68
70	9	31.6	56.2	64.6	70.1	72.2	25	25	25	25
71	6.2	9.2	22.4	23.5	27.1	28.5	35	53.3	58.4	87.1
72	14	31.4	41.1	41.5	42	44.7	25	25	25	5000
73	9.8	26.5	27.3	29	35.9	77.5	25	25	25	25
74	5000	5000	5000	5000	5000	5000	5000	5000	5000	5000
75	9.6	19.2	31.6	33.8	38.5	47.6	53.9	53.9	53.5	53.5
76	8.4	24.2	36.4	37.5	41.8	50.2	25	25	25	5000
77	14.9	40.5	26	24	30.7	44	25	25	25	25
78	10.5	33	45.1	47.5	51.3	56.6	66.6	66.5	66.5	66.5
79	11.3	26.9	42	42	51.2	68.2	25	25	25	25
80	15.4	41.4	50	51	51	51	5000	25	5000	5000
81	5000	42.4	24.3	29	70.9	86.4	105.1	5000	5000	104.2
82	7.5	14.2	23.3	23.6	25.8	33.5	25	25	25	25
83	6.5	22.4	32.8	32.6	39.1	40.2	5000	5000	5000	5000
84	7.9	17.1	36.4	36.9	41	50.6	51.2	52.1	52	52
85	8.5	15.2	26.6	27	34.5	34.7	25	25	25	5000
86	5.1	15.6	32.3	34.9	22.3	22.5	45.4	45	45	45.8
87	12	24	38.4	38.8	45.8	56.8	57	57	57	57
88	10	22	22	22.1	47.8	66.8	33	35.4	35.3	35.2

89	11.1	30	45.1	48.3	57.2	73.5	25	25	25	25
90	10.2	23.9	32.5	34.3	38.6	50.5	57	57	57	5000
91	12.7	31.1	45.8	50.5	55.6	62.6	25	25	25	5000
92	6	4.8	12.6	16.5	16.3	16.5	17.2	17	5000	5000
93	6.8	14.5	27.2	28.1	28.9	32.5	32.9	36.5	36.7	37.3
94	8	23.2	39.1	42.4	51.9	69.5	25	25	25	25
95	14.3	30.7	35.7	35.5	36	38.5	39.9	53.5	74.9	85
96	7.4	24.6	45.2	36.2	36.6	37	62.1	62.3	63.5	64.4
97	9.4	34.3	36	36.3	46	46.7	25	25	25	25
98	3.5	16.8	24.5	24.5	30.3	46.6	25	25	25	25
99	8.5	14.6	24.2	25.3	25.6	25	28.1	28.2	28.2	28.2
100	8.6	20.8	36	37	43.8	57.3	25	25	25	25
101	9.3	20.6	34.3	34.8	36.2	36.5	25	25	25	25
102	11.6	32.5	57.3	59.5	68.3	77	97.6	97.9	97.7	95.7
103	24.4	17.9	18.1	18.2	26.1	40.4	25	25	25	25
104	5.5	30	54.9	59.7	61.4	76.5	25	25	25	25
105	8	8.8	10.4	27.6	32.2	43.7	71.8	72	72	72
106	5000	5000	31.7	32.3	37.8	53.5	38.4	38.2	38	38
107	5000	5000	27	28	34.5	34.7	26.5	30.6	30.6	30.6
108	5000	5000	28	28.8	35.2	46.3	46.3	47.3	55.8	55
109	5000	5000	23.4	24.7	30.3	39.7	5000	25.5	27.6	28.5
110	5000	5000	17.4	17.8	27.2	41.7	25	25	25	32
111	5000	5000	13.3	38	42.2	52.8	53	53.4	53.4	53.4
112	5000	5000	38.7	38.8	44.2	52	25	25	25	25
113	5000	5000	36.7	36.9	39.4	39.5	25	25	25	25
114	5000	5000	35.2	37.7	41.7	46.1	46.2	46.8	46.8	5000
115	5000	5000	25.8	25.8	34	34.5	25	33.7	51.9	61.5
116	5000	5000	49.5	50	50.4	67.6	25	25	25	5000
117	5000	5000	29.5	30	34	50.4	25	25	25	36
118	5000	5000	43.6	45	52.6	68.1	68.6	68.6	5000	5000
119	5000	5000	30	32.6	36.6	54.5	25	25	25	5000
120	5000	5000	37.5	40	46	59.9	60	60	60	60
121	5000	5000	38.6	31	30	31	25	36.9	31.3	28
122	5000	5000	11.5	39.9	46.3	49.8	50	50	50	50
123	5000	5000	55	56.6	68	73.6	25.3	25	25	25
124	5000	5000	25.8	27.5	36	63.7	84.3	91.1	94.4	94
125	5000	5000	33	33	41.4	55	56.6	56.5	56.5	56.5
126	5000	5000	26	28	37.6	58.3	71.2	72.3	72.3	73.2
127	5000	5000	34.7	37	42.1	60.2	65.7	66.3	66.2	5000
128	5000	5000	47.5	49	57.4	83.2	99	100.5	100	100
129	5000	5000	5000	5000	5000	5000	5000	5000	5000	5000
130	5000	5000	37.6	40.1	43.5	49.6	56.2	25	25	25

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	124	130	138	144	151	159	167	173	180	187
1	9.2	22.6	41	42.8	45.6	50.8	25	25	25	25
2	8	18.9	32.9	32.8	37.3	43.8	25	25	25	25
3	5.2	11.6	19.8	20.5	22.5	37.7	40	40	39.5	39.5
4	18.6	42.1	62.2	62.5	64	75.1	25	25	25	5000
5	5.6	10.7	20	21.2	27.4	40.7	25	25	25	5000

6	11.9	29	34.4	34.6	34.7	41.8	87.5	88.6	88.3	88.2
7	8.9	14.3	27.1	29	31.1	32.1	25	25	25	25
8	7.1	15.6	32.1	32.9	39.2	52	25	25	25	25
9	8.8	20.5	35.7	37.4	38.3	43.1	25	25	25	5000
10	8.9	19.5	35	36	41.5	57.8	63.6	65.5	66.4	67.7
11	18.2	37.8	57.5	58.1	64.2	77.6	32.4	39.3	43.4	44.3
12	8.2	22.1	35.6	37.7	44	56.2	25	25	25	26
13	5	5	6.2	6.8	7.8	13	13	13.7	13.6	22.5
14	12.9	19.6	24.3	25.5	27.6	28	28	28	28	27.5
15	9.1	24.3	39.9	39.4	43.2	58.4	59.2	63	65.6	65.5
16	15.4	15.5	25.4	25.5	31.1	50	25	25	25	25
17	12.5	13.5	13.2	13.7	13.4	13.8	27.3	42	48.8	49.4
18	2.5	18	34.9	36	46.6	59.2	61.1	75.5	76.1	77.2
19	6	21.7	40.7	40.8	47.2	63.4	25	25	25	25
20	14.5	31.5	47.7	48	48	57.5	25	25	25	25
21	5.8	26.2	52.8	55.5	63.4	82	92	92	92	92
22	6.5	20.8	32.9	34	34.6	36.3	25	25	25	25
23	13.4	15.5	15.9	15.8	16.2	30.5	25	29.6	35.4	36.5
24	12.1	34.1	50.3	50.7	55.5	58.8	69.1	80.4	87.3	87.5
25	24.4	45.4	66.2	67.5	76.6	97.2	30.7	30.5	31.5	32.5
26	8.2	17.5	27	28.6	34.7	48.1	25	25	25	25
27	10.9	22.8	51.3	52.9	53	53	53	53	53	53
28	5	21	35.6	37	37	57.1	25	27	28	28
29	4.9	10.1	21.5	22	24.7	26	25	25	25	25
30	12.5	14.5	15.3	15.8	5000	5000	5000	5000	5000	5000
31	15	27.2	47.1	48.9	48.9	66.7	25	25	25	25
32	10.2	13.2	28.8	29.4	37.4	57.9	25	25	25	25
33	15.2	20.9	36.1	36.8	43.5	64.1	70	70	71.2	71
34	13.5	17	23.5	23.5	28.7	85.7	25	25	25	25
35	12.4	12.4	31	31.7	31.7	36.7	25	27.2	33.6	33.5
36	15.8	28.7	45	45	45	70.3	97.5	107.2	107	107
37	11.9	27.1	45.6	46.7	53.2	68.1	25	25	25	25
38	15.3	40.4	65.8	68.5	74.6	101.4	25	25	25	25
39	12.2	30.3	45.5	45.5	52.2	72.2	80.7	80.5	80.5	81.5
40	21.1	45.2	64.9	67.6	72.5	94.3	25	25	25	25
41	9	18.8	22.7	23	23	23.1	23	23	23	23
42	7.1	22	22	27.4	42	55.3	25	25	25	25
43	8.8	16	27.4	28.3	34.1	42.8	25	25	25	5000
44	8.7	14.7	27.3	27.9	28.5	42.4	25	25	25	26
45	6.5	12.3	19.6	20.4	23.8	37.6	44	42.3	42.8	47
46	11.2	22.6	35.9	37.5	40.1	55.2	25	25	25	25
47	8	10.8	16.6	17.4	20.9	32.3	25	25	27.5	30
48	10.6	17.3	25.7	26.3	28.1	31.9	32	32	32	32
49	10.8	31.5	48.5	48.8	51.9	56.2	25	25	25	25
50	8	14.5	24.6	25.3	27	33.1	25	25	25	25
51	11.8	11.8	11.9	12	12	12	12	12	5000	5000
52	6.4	14	21.8	22	25.2	31.8	25	25	25	25
53	12.4	25.8	38.2	46.4	49.7	68.2	25	25	25	25
54	11	15.6	21.3	24.2	27.4	41.5	49.3	58	67.2	67.3
55	11.1	20.3	29.7	31.6	32.1	40.2	25	25	25	26
56	5.9	9.4	10.2	11.2	11.3	11.2	11	11	11	34.5
57	19.2	27	38.1	39.8	39.8	46.6	25	25	25	25

58	17.2	31	43.2	44.7	50.1	66	25	25	25	25
59	11	20	27	33	38.8	54.2	25	25	25	25
60	16.4	26.5	26.5	26.5	26.8	26.8	25	25	25	25
61	13	28.2	41.9	42.5	51.2	69.4	25	25	25	26
62	10.9	23.7	40.6	43.4	46	64.4	25	25	25	25
63	10.3	19.6	31.6	33.3	36.7	37	37.7	37.7	37.3	37.3
64	18.1	32	49	50.4	52.7	52.2	35.6	72.4	72.6	5000
65	33	53.9	72	75.7	83.2	109	25	25	25	26.5
66	8.7	5000	38.7	41.5	47.1	56	56.2	58	57.9	59.7
67	5.8	20	26.2	27.5	33.5	47.8	25	25	25	25
68	14.8	28	38.9	40.4	45.1	60.7	25	25	25	25
69	8.1	14.1	25	25.6	29.9	45.2	25	25	25	26
70	10.7	31.1	49.1	51.3	54.6	61.2	25	25	25	46
71	15.3	28.3	34.6	34.8	33.3	43.4	25	25	25	25
72	8.5	16.9	23.3	25	27.4	29.6	29.7	29.7	29.6	29.5
73	10	21.6	31	31.4	35.1	35.4	25	25	25	25
74	4.5	9.5	15.8	16.8	22.5	23.6	25	25	25	44.2
75	7.5	16	30.1	30.5	32.4	34	45.1	52.1	54.8	55
76	7.3	13	13.6	13.5	13.4	13.4	16.5	16.5	16.5	19.5
77	15	29.5	44.4	46.5	50.1	57.3	25	25	25	30
78	10	20.6	35.8	38	38.5	46.2	25	25	28	47
79	9	20.3	36	38	47	50.1	52.7	25	25	25
80	9.5	29.9	37.7	39.1	47.4	71.5	25	25	25	25
81	7.8	7.6	8.2	8	8	25.7	32.2	36.2	36.7	36.5
82	14.5	32	51.9	53	61.7	78.3	25	25	25	5000
83	11.2	14	14.4	14.6	15.1	23.1	29.2	29.2	29.1	29
84	5	6.5	12.9	11.5	13.5	13.5	13.5	13.5	13.5	13.5
85	12.2	22.3	33.6	35	37.3	48.2	25	25	25	25
86	14.9	33.5	43.4	45.6	51.9	66.7	25	25	25	5000
87	9.3	23.2	34.4	35.2	41.9	58.2	67.3	67.3	68.5	69.3
88	9.6	23.8	34.5	38.5	41.1	62.4	25	25	25	25
89	9.4	29.2	43.1	44	37.3	55.4	25	25	25	25
90	9.8	19.1	27.2	28.2	31.6	44.7	50.5	50.5	57.6	58.4
91	7.8	20	30.8	32.5	37.5	58.9	25	25	25	25
92	13.9	23.8	25	27.7	30.1	43.4	25	25	25	25
93	8.4	19.7	29.4	29.8	30.5	33.8	34.2	24	5000	5000
94	5000	5000	5000	5000	5000	5000	5000	5000	5000	5000
95	13.5	28.9	43.4	45.2	49.2	68	25	25	25	25
96	3.4	6.3	6.3	6.4	9.9	16.4	18	26.5	26.5	27.3
97	8.4	18.2	28.5	30.2	51.5	51.5	25	25	25	25
98	8	10.6	10.5	10.5	11.9	12.2	12.2	13.2	13.2	20
99	4	10.8	15.6	16.4	19.7	33.3	31.3	5000	5000	5000
100	8.5	18.5	30	30.9	39.2	69	25	25	25	25
101	8	17	29.6	30.5	31.4	32.6	25	25	25	5000
102	3.7	13.7	25	26.3	31.4	53.7	25	25	25	25
103	15.3	27.7	41.3	42.2	35.6	65.4	25	25	25	25
104	10.7	17.8	32.2	33	38.2	50.1	25	25	25	5000
105	9.6	22.3	39.3	40	41.7	58.9	25	25	25	25

Site P3

	130	138	144	151	159	167	173	180	187
1	19.9	27	28.8	34.2	49.6	25	25	25	25
2	17	28.3	31.9	38	55	25	25	25.5	25.5
3	25.4	39.1	43.5	48.7	66.4	25	25	25	25
4	27.3	34.7	33.9	36.7	39.8	36.9	37.2	50	50
5	27	37.8	43.5	49.5	58	25	25.7	25.5	43.3
6	20.4	31.9	34.2	38.5	46.8	50.6	50.6	5000	51.4
7	20	36	41.3	52.2	71.1	25	25	25.5	25.5
8	37.5	48	48	48.7	50.4	42	48.6	48	48
9	25.3	32.8	32.5	39.4	49.1	53.5	53.8	54.5	54.5
10	23	29.7	29.7	34.5	45	25	25	25	25
11	26	33.2	33.5	34.1	34.1	25	25	25	26
12	17.6	23.6	23.8	25	25.4	31.5	35.3	44.2	58
13	13.7	14.4	14.7	16.5	16.5	16	16	16	16
14	21.4	34.1	33.5	40.5	40.3	25	25	25	25
15	11.6	22.3	22.3	28.1	39	39	39	38.8	39
16	24.1	39.7	41.4	50.4	63.1	25	25	25	25
17	24.9	29.8	38.4	38.4	38	25	25	25	25
18	26	36.1	36	48.3	53	58.1	57.9	58	58
19	20.4	33.1	33.5	38.6	45.3	25	25	25	25
20	33.4	39.1	39	39	43.7	25	25	25	5000
21	14.6	20.3	20.2	23.3	23	30	29.2	29	29.2
22	19.8	30.5	33.5	38	54.5	25	25	25	25
23	8	10.8	11	11	11	11	11	18.5	53
24	14.7	17.7	19.2	23.7	33.7	36.5	39.7	5000	40.3
25	18.1	31	32.4	35.4	59.1	25	25	25	25
26	18.5	25.5	17	17.2	17.2	17	5000	5000	5000
27	15	15	15	15.6	16.3	17	17	34	54.5
28	18.6	28.9	29.2	34.7	52.9	25	25	25	25
29	18.2	28	28.8	33.7	45	25	25	25	25
30	26.3	35.5	39	48.4	64	25	25	25	25
31	38	41.5	41.7	43.9	57.7	25	25	25	25
32	35.5	52.1	56.1	60	64.5	25	25	26.5	26.8
33	28.3	32.2	36.9	38.8	47	25	39.6	39.5	39.5
34	16	24.7	26.9	28.1	30.3	43.2	43	43	43
35	27.2	39.1	40.2	50.7	59.4	25	25	25	37
36	23.6	31	34.9	40	51.5	61.5	68	73.5	5000
37	37	55	55	61.4	71	25	25	25	25.5
38	22.4	35	35	38.5	47	25	25	25	25.5
39	26.7	42.3	41.9	47.2	59.8	70.4	70.3	70.2	70.3
40	10.8	15.6	15.2	18	22.5	24.7	25.2	25.4	25.5
41	15.3	18.9	21.6	24.8	25	25	25	25	25
42	18	20	26.5	31.5	47.1	25	25	25	25
43	10.2	13	13.4	16.6	18.8	23	23.2	23.5	23.5
44	11.8	16.5	17.1	17.9	18.9	18.6	18.5	18.5	18.5
45	18.7	24.1	24.5	28.4	33.1	25	25	25	25
46	11.6	13.3	13.3	13.5	13.7	13.5	13.5	15.5	21.4
47	15	18.7	19	21.8	30.2	25	25	25	36.3

48	11.3	14.2	14.7	18.5	19.6	26.6	27	28.2	29
49	28.3	40.6	40	51.7	67.4	25	25	25	25
50	23.3	32.9	35	39.5	55	25	25	25	25
51	23.7	37	37.7	52.8	59.5	25	25	25	25
52	30.2	48.4	53.6	60.2	62.1	25	25	25	25
53	30.8	30.3	30.3	32.4	48.5	35	36.3	43.5	43.5
54	30.7	45.1	47.9	58.2	83.9	91.2	94.4	95.5	95.5
55	27	40.5	42.8	46.7	54.3	25	25	25	25
56	17.3	25.1	26.7	34.2	46.2	25	25	25	25
57	23.7	44	44	57.3	76	91.6	94.4	95	96.5
58	16	24.7	26.4	35.8	43.5	25	25	25	25
59	18.2	28.6	31.1	38.6	47.8	25	25	25	25
60	19.1	28.1	29.6	55.5	55	69.6	69	69	69
61	21.8	38	39.4	47.3	67.5	25	25	25	25
62	16.3	24.9	26.7	30.8	31.4	25	25	29.5	29.5
63	37.6	52.3	55.9	56	83	25	25	25	25
64	11.2	18.6	20	21.6	21.3	41.4	45.1	45	45
65	28.2	45.2	45	49.2	68.7	25	25	27	27
66	16.9	23.9	25.2	32.8	44.5	54.8	56.6	56.5	57.3
67	26	37	41.7	45.7	59.5	25	25	31	31
68	25.3	59	71	73.4	93.3	25	25	25	25
69	12.7	22.3	24.8	31	47	56.7	62.4	63.8	66.5
70	18.3	32.8	33	40	50.4	25	25	25	25
71	29.3	30.4	34	34.2	34	25	25	25	25
72	27	39	41.3	46.9	61	65.6	65.1	65.5	65.2
73	17.8	17.5	17.8	26.4	38.4	25	25	25	25
74	29.4	43.5	43.5	43.5	55.7	25	25	26	48
75	18.3	23.3	26.5	29	40.2	25	25	25	25
76	19.9	24	26.2	29	28.5	25	25	25	25
77	17	29.7	30.9	34.8	45.6	25	25	31	31
78	25.1	39.5	39.9	52	68.5	84.1	85.1	85	86
79	18	25.1	25.3	30	33.4	25	25	25	25
80	22.3	28	29.5	35	40.1	25	25	25	25
81	8.2	10.7	10.7	11	10.7	11	11.7	11.5	5000
82	16.7	19	19	24.9	30	25	25	25	25
83	5.9	10	10.5	10.2	12.5	22.5	31.9	32	32
84	16.7	22.7	25.4	32.4	41.5	54.3	54.3	55	57
85	26.2	41.7	48.7	57	77	25	25	33.1	33
86	25	33.7	38.8	43.6	49.1	25	25	32.3	32
87	17.6	24	24	30	41.5	44.5	44.7	44.2	45.5
88	18.5	24	25.5	33	44.2	25	25	25	25
89	5000	5000	5000	5000	5000	5000	5000	5000	5000
90	12.2	19.2	20.7	25.7	40.9	25	25	25	25